

## HOW MUSCLES DEAL WITH REAL-WORLD LOADS: THE INFLUENCE OF LENGTH TRAJECTORY ON MUSCLE PERFORMANCE

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### Summary

The performance of skeletal muscles *in vivo* is determined by the feedback received when the muscle interacts with the external environment *via* various morphological structures. This interaction between the muscle and the 'real-world load' forces us to reconsider how muscles are adapted to suit their *in vivo* function. We must consider the co-evolution of the muscles and the morphological structures that 'create' the load in concert with the properties of the external environment. This complex set of interactions may limit muscle performance acutely and may also constrain the evolution of morphology and physiology.

The performance of skeletal muscle is determined by the length trajectory during movement and the pattern of stimulation. Important features of the length trajectory include its amplitude, frequency, starting length and shape (velocity profile). Many of these parameters interact. For example, changing the velocity profile during shortening may change the optimum values of the other parameters.

The length trajectory that maximizes performance depends on the task to be performed. During cyclical work, muscles benefit from using asymmetric cycles with longer

shortening than lengthening phases. Modifying this 'sawtooth' cycle by increasing the velocity during shortening may further increase power by augmenting force output and speeding deactivation. In contrast, when accelerating an inertial load, as in jumping, the predicted 'optimal' velocity profile has two peak values, one early and one late in shortening.

During level running at constant speed, muscles perform tasks other than producing work and power. Producing force to support the body weight is performed with nearly isometric contractions in some of the limb muscles of vertebrates. Muscles also play a key role in producing stability during running, and the intrinsic properties of the musculoskeletal system may be particularly important in stabilizing rapid running. Recently, muscles in running invertebrates and vertebrates have been described that routinely absorb large amounts of work during running. These muscles are hypothesized to play a key role in stability.

Key words: contractile properties, power output, work loop, jumping, running, stability, velocity-dependent activation.

### Introduction

#### *The nature of the problem: muscles and their loads*

For years, students have been introduced to the function of muscle during movement by descriptions of isotonic loading in which the load remains constant as the muscle shortens (Fig. 1). Leaving aside the fact that what is depicted in Fig. 1 is actually a rather poorly designed isotonic lever, we can ask how this simple loading regime constrains our view of muscle function. In isotonic loading, the properties of the muscle determine how fast and how far the muscle will shorten. Depending on the conditions employed, these properties will include the force–velocity relationship, the length–tension relationship and the kinetics of activation and deactivation. Series elastic elements typically play no role because, once the muscle begins to move the load, the force on these elements remains constant during shortening. Despite the almost universal realization that this type of loading is unrealistically simple, thinking about muscle and movement has been influenced extensively over the

years by the constraints inherent in isotonic loading. Discussions have often focused on how muscle properties are matched to the load with less thought given to how evolution has also matched the load to the properties of muscle.

During *in vivo* movements, muscles seldom, if ever, act on loads that are constant (Fig. 2). Muscles can contract against five basic types of loads: gravitational, elastic, inertial, viscous and drag. Of course, the load faced by the muscle may be a combination of two or more of these basic types of loads, and the quantitative importance of the various types may change during the movement. Of the five types, only gravity imposes a load that is expected to be constant during the movement. Even in this case, the load experienced by the muscle is often not constant because of changing mechanical advantage during the movement.

For most realistic conditions, the movement itself creates changes in the load. When shortening stretches an elastic

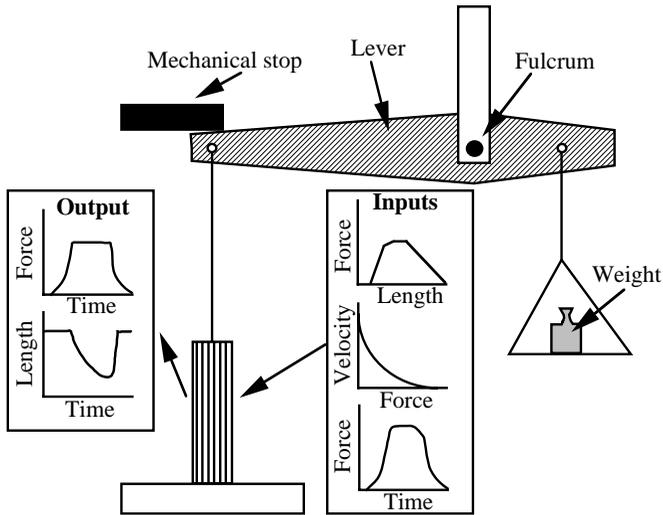


Fig. 1. Schematic diagram of isotonic loading. The movement of the load (output on the left) is determined directly by the underlying properties of the muscle (inputs on the right).

structure in series with the muscle, the force increases with the distance shortened. The load created by viscosity increases in proportion to the velocity of shortening of the muscle. Moving a mass imposes a load on the muscle proportional to the rate of change of velocity or acceleration. The force required to overcome drag varies in proportion to velocity raised to a power of between 1 and 2 depending on the Reynolds number at which the morphological structures interact with the fluid environment. Not included in this list, and harder to specify, is the load created when a muscle stretches another active muscle. The stretched muscle exhibits complex nonlinear changes in force with the velocity of stretch (Josephson, 1999).

The changing force during the movement feeds back onto the output of the muscle (Fig. 2). The nature of some of this feedback is predictable in terms of force-velocity and length-tension effects (Askew and Marsh, 1998). As the velocity of the muscle changes during the movement, force will change as a result of force-velocity effects, and as the muscle shortens, the maximal force production will change as a result of length-tension effects. Although these effects are

straightforward to understand, recognizing them in an *in vivo* setting may be challenging because of other effects operating during cyclical contractions (e.g. Marsh and Olson, 1994; Askew and Marsh, 1998).

In many cases, the basic properties of muscle seem at odds with the properties of the load (Marsh, 1990; Daniel, 1995). For many types of load (Fig. 2), force tends to increase as a function of velocity. Clearly, this requirement contradicts the force-velocity properties of muscle, which dictate that force must decline with increasing velocity (given constant activation). Also, if a muscle stretches an elastic element by shortening below optimum length, the requirement for increasing force as shortening proceeds contrasts with the decreasing ability to produce force at short lengths. These conflicts set limits on muscle function and have probably had major influences on the evolution of the locomotor morphology that couples the muscle to the load (Daniel, 1995).

Additionally, the movement may actually alter some of the properties of muscle that help determine performance. For example, shortening or lengthening an active muscle results in changes in the kinetics of activation and deactivation (Askew and Marsh, 1998) and in changes in the steady-state force production (Josephson, 1999). These changes are not completely understood, and many experiments performed *in vitro* are difficult to interpret in terms of *in vivo* conditions.

A further complication for *in vivo* muscle function is the influence of the morphology of the locomotor system that is interposed between the muscle and the environment on which it operates (Fig. 2). In fact, although Fig. 2 depicts the morphological structures as being between the muscle and the load, this distinction is more conceptual than real. In many cases, these structures help determine the nature of the load. As the movement proceeds, the morphology may alter its shape which, in turn, influences muscle function as the interaction with the environment changes. Examples include the interaction of fins and wings with the surrounding water or air and the changing mechanical advantage as the limbs of a jumping animal unfold.

This complex scheme presents us with the challenge of understanding the co-evolution of the properties of muscles and the morphological structures to which they are coupled. Muscles do not produce movements in a straightforward way. Instead, the movement and, therefore, the performance of the muscle result from an interaction between the muscle, the locomotor morphology and the characteristics of the load. For example, it has been found that the muscles of swimming fish and calling frogs contract over a range of velocities expected for optimizing power output (Rome et al., 1988; Girgenrath and Marsh, 1997, 1999). To what extent then can we talk about the force-velocity properties of these muscles being matched by evolution to meet the functional demands of the movement? Selection could also operate on the shape of the fins and the mechanical advantage of the myotomal muscles in the swimming fish or on the elastic properties of the vocal sac and on the resistance to air flow in the calling frog to produce a load that matches the force-velocity characteristics of the muscles. Clearly, selection can and does operate at both levels.

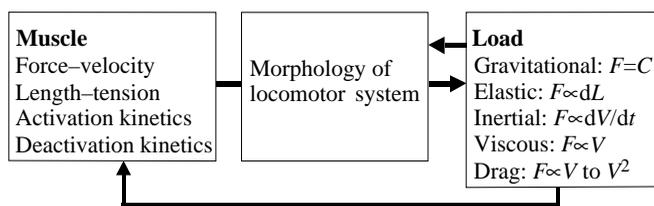


Fig. 2. Real-world loads. During natural movements, the type of load is in most cases influenced by the movement. The changing load feeds back onto the muscle, altering its output. The load also interacts with the morphological structures interposed between the muscle and load. These structures may change shape during the movement, altering this interaction.  $C$ , constant;  $F$ , force;  $V$ , velocity;  $dL$ , change in length;  $dV/dt$ , acceleration.

*Approaches to understanding the problem*

How can we increase our understanding of this complex problem? One approach is to attempt to model specifically the system of interest from the level of the muscle to the external environment (Zajac and Winters, 1990; Daniel, 1995). Such models are valuable, but their utility is dependent on our understanding of their various components. Considering the properties of muscle, these models have often been limited by the use of data from simple *in vitro* contractile studies. Such studies reveal much of value about muscle function, but may be problematical when applied to the complex regime of loading and movement found *in vivo*. Data exist on muscles subjected to more complex loading regimes, e.g. quick stretches and quick releases, but how this information relates to *in vivo* muscle use is often unclear.

Further progress in understanding the mechanical function of muscle *in vivo* is dependent on increasing our knowledge of the activity and shortening of individual muscles during natural movements. Without knowing how muscles are used *in vivo*, we simply do not know what *in vitro* experiments need to be performed. Once information is available on the function of individual muscles during natural movements, it can then be coupled with appropriate *in vitro* measurements to test hypotheses about which properties of muscle are most important for determining function.

**Estimating muscle performance *in vivo****Direct in vivo measures of length and force*

A fairly complete picture of the performance of individual skeletal muscles can be obtained *in vivo* in those cases in which both muscle fiber (fascicle) length and force can be recorded simultaneously. Muscle fiber length can be measured directly using sonomicrometry, a technique in which pairs of ultrasound crystals are implanted along the fibers. This technique, originally developed for acute experiments on the heart (Rushmer et al., 1956), has been difficult to implement in the skeletal muscles of freely moving animals. One of the earlier uses was by Hoffer et al. (1989). Recent studies have been successful in recording high-quality data at least partly as a result of improvements in implantation techniques. In conjunction with sonomicrometry, force has been estimated using tendon buckles (Hoffer et al., 1989; Biewener et al., 1998b), strain gauges on bony elements (Roberts et al., 1997; Biewener et al., 1998a) and pressure (Marsh et al., 1992).

The number of muscles for which recordings of both force and length have been successfully combined is limited. Examples include the adductor muscle of scallops (Marsh et al., 1992; Marsh and Olson, 1994), the lower leg muscles of running and hopping vertebrates (Roberts et al., 1997; Biewener et al., 1998b) and the pectoralis muscle of flying birds (Biewener et al., 1998a). Additional studies of the function of the cat ankle extensor muscles have used tendon buckles for measuring force and filming to estimate length changes in the muscles (Whiting et al., 1984; Prilutsky et al., 1996). However, when using filming to predict muscle length,

the many steps and assumptions necessary to convert external movements to muscle fiber strain may make determination of the details of the length trajectory difficult. The use of filming to measure strain is less complicated in studies of the myotomal muscle of swimming fish and the trunk muscles of calling frogs because the geometry is simpler (Coughlin et al., 1996; Girgenrath and Marsh, 1997; Katz et al., 1999).

A serious problem with extending *in vivo* measures of performance to a wider variety of muscles is the limited number of muscles for which one can record force. Apart from pressure–volume systems, e.g. scallop swimming, successfully recording force requires a muscle that has a long tendon or is attached to a bony process that is uniquely strained by the muscle. These requirements limit the muscles on which force measurements can be obtained.

*Integrating in vivo and in vitro studies*

An alternative approach to estimating muscle performance involves combining *in vivo* and *in vitro* measurements. Using this approach, *in vivo* measurements of the muscle's activation pattern obtained using electromyography and length trajectory obtained using sonomicrometry or high-speed filming are used to design *in vitro* experiments that measure performance under conditions that replicate those occurring *in vivo*.

A diverse set of factors affect the work and power output of skeletal muscle (Josephson, 1993). However, all these factors can be lumped into two: the pattern of stimulation (phase and duration) and the strain trajectory (amplitude, starting length, frequency and cycle shape). Thus, *in vivo* function can be estimated by measuring the *in vivo* length change and stimulation pattern and using these measurements to design *in vitro* experiments that replicate the *in vivo* conditions as closely as possible. The muscle then integrates the various inputs and performs as it does in the intact animal.

Replication of the *in vivo* strain trajectory and stimulation pattern was developed as an extension of the work loop approach (Marsh et al., 1992; Marsh and Olson, 1994). Scallops were chosen as an initial test of this method because the power output could also be estimated during natural swimming (Marsh et al., 1992). We found that we could replicate the distribution of power during the cycle quite precisely. Subsequent work has confirmed the continued usefulness of this approach (Rome et al., 1993; Franklin and Johnston, 1997; James and Johnston, 1998; Full et al., 1998; Girgenrath and Marsh, 1999). This integrated approach uses information about *in vivo* function to design appropriate *in vitro* experiments and information gained *in vitro* to predict how muscles should behave to optimize diverse *in vivo* functions.

**The strain trajectory and muscle function during movement***Cyclical production of work and power*

The most obvious function of muscles during movement is to provide the work and power that create the movement. The clearest examples of the cyclical production of work and power

come from non-terrestrial locomotion and sound production. During swimming and flying, muscles function to overcome the drag of the medium and to produce lift, and these functions require the continuous production of power (Altringham and Johnston, 1990; Marsh et al., 1992; Rome et al., 1993; Biewener et al., 1998a). During sound production, muscle work is converted to sound energy (Rome et al., 1996; Girgenrath and Marsh, 1997, 1999).

Much has been learned about the function of muscles in cyclical contractions by using *in vitro* work loop studies with optimized sinusoidal length trajectories (Josephson, 1993). Recent *in vitro* studies have also used length trajectories derived from *in vivo* measurements. Work on scallop adductor muscle demonstrated that using the naturally occurring length trajectory resulted in the production of approximately the same average power as sinusoidal cycles, but that the distribution of power during the cycle was quite different (Marsh et al., 1992; Marsh and Olson, 1994). However, more recent work on other systems indicates that other cycle shapes provide considerable enhancement of performance over that found during sinusoidal cycles.

Recent studies have shown a substantial advantage in power output of using asymmetrical 'sawtooth'-shaped cycles in which the shortening phase takes longer than the lengthening phase. These cycles were first observed in my laboratory in studies of the muscles used for calling in tree frogs (Fig. 3) (Girgenrath and Marsh, 1997). *In vitro* studies demonstrated that this cycle shape provides considerably more power at the natural operating frequency than does a sinusoidal trajectory (Fig. 4) (Girgenrath and Marsh, 1999). Taking advantage of the flexibility of *in vitro* studies, Askew and Marsh (1997) used mouse soleus and extensor digitorum longus muscles to document systematically the advantages of the sawtooth cycle. They showed that a key to the enhancement of performance is the longer shortening time. During sawtooth length trajectories, the power output of these mouse muscles increased as the proportion of the cycle spent shortening increased. The increase in power is attributable to more complete activation of the muscle as a result of the longer stimulation duration, a more rapid rise of force as a result of

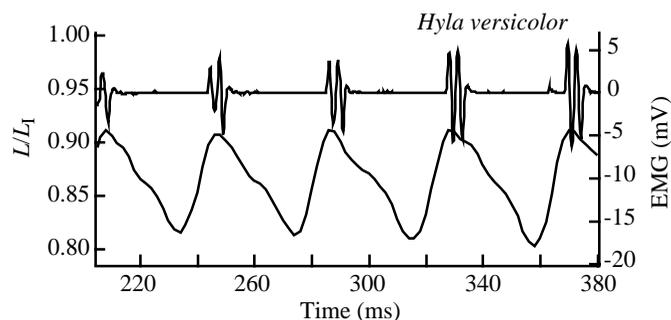


Fig. 3. Muscle strain and electromyographic activity of the external oblique muscle in a calling gray tree frog *Hyla versicolor* (from Girgenrath and Marsh, 1997).  $L$ , muscle length;  $L_1$ , initial muscle length just before the call; EMG, electromyographic activity.

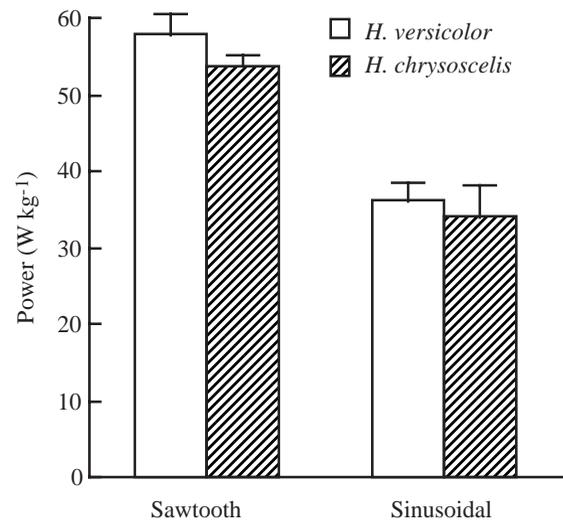


Fig. 4. Power output of the external oblique muscles of the gray tree frogs *Hyla versicolor* and *Hyla chrysoscelis* (from Girgenrath and Marsh, 1999). Muscles were subjected *in vitro* to both sinusoidal and sawtooth cycles. The sawtooth cycles represented simplified versions of the *in vivo* strain trajectory. Values shown are means + S.E.M. for five muscles.

increased stretch velocity and an increase in the optimal strain amplitude. The performance enhancement due to asymmetrical cycles can only be realized in morphological systems in which movement in one direction represents the power stroke and the recovery stroke is passive or lightly loaded. Examples of such systems include bird flight, frog calling and scallop swimming. For systems constrained to operate with power output in both directions of movement, e.g. fish swimming, symmetrical cycles provide equal performance for both opposing sets of muscles.

*In vitro* studies on mouse muscles using sawtooth cycles have also demonstrated the effects of feedback on muscle properties from the velocity of lengthening and shortening (Askew and Marsh, 1998). These authors found that, at low frequencies, the output of the muscle was predictable from a simple model. The calculated curve was derived from a model incorporating length-tension and activation kinetics from isometric contractions and force-velocity effects from isotonic contractions. However, at high frequencies, this model did a poor job of predicting performance (Fig. 5). The discrepancies between the model and the data were ascribed to the effects of the velocity of lengthening on the rate of activation and of the velocity of shortening on the rate of deactivation.

The results from these studies on mouse muscles suggest that power may be increased by lengthening as rapidly as possible to enhance activation. Further improvement in performance may come from accelerating during the latter part of shortening to enhance deactivation. Unpublished work by G. Askew and myself on the pectoralis muscle of quail during vertical flights suggests that the strain cycle for this muscle meets these criteria. *In vitro* studies demonstrate that the slight deviations of this length trajectory from simple constant-

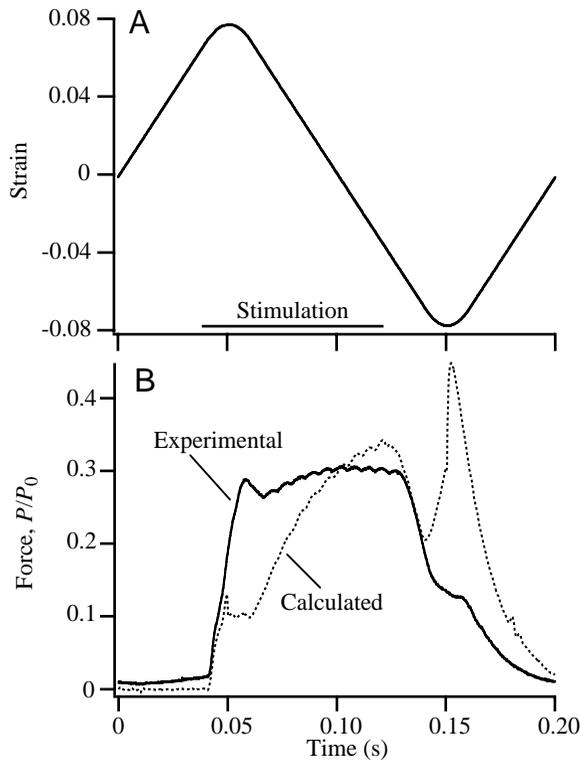


Fig. 5. Performance of mouse soleus muscle at 5 Hz (from Askew and Marsh, 1998). (A) Strain cycle and stimulation pattern. (B) Experimentally determined and calculated force output. The calculated curve was derived from a model including length–tension and activation kinetics from isometric contractions and force–velocity effects from isotonic contractions. The difference between the calculated and measured curves was ascribed to differences in the kinetics of activation and deactivation between isometric and cyclical contractions.  $P/P_0$ , force as a fraction of maximum isometric force.

velocity shortening enhance force and therefore power during shortening by approximately 20%.

#### Work and power output in single contractions

Terrestrial animals that jump from a stationary position use many of their hindlimb muscles to produce the necessary acceleration to propel the body off the ground (Bennet-Clark, 1977; Edgerton et al., 1986; Marsh, 1994; Aerts, 1998). Theoretical and empirical studies suggest that the rules for maximizing performance under these conditions may be different from those in cyclical contractions. Maximizing work output during the take-off phase of the jump maximizes jumping distance. However, because of the fixed geometry of the legs, maximizing work also necessitates producing very high power output during this same period (Marsh, 1994). Measurements indicate that the peak power greatly exceeds that available from the hindlimb muscles (Peplowski and Marsh, 1997; Aerts, 1998). It has been suggested that elastic storage plays a key role in this enhancement of performance (Peplowski and Marsh, 1997).

The change in force and power output during the jump

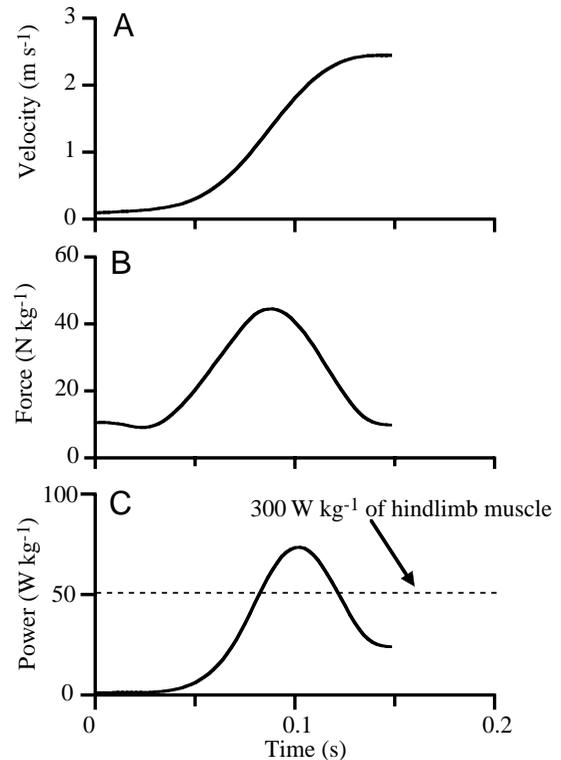


Fig. 6. Dynamics of take-off in a 0.85 m jump of a bullfrog *Rana catesbeiana* measured from high-speed video recordings (T. Roberts and R. Marsh, unpublished results). (A) Velocity of the center of mass. (B) Ground reaction force. (C) Power output. The dashed line shows the maximum power output of the hindlimb muscles based on the generous estimate of  $300 \text{ W kg}^{-1}$  of hindlimb muscle (see Olson and Marsh, 1998). The 0.85 m jump is considerably shorter than the measured peak jumping distance for this species.

measured at the level of the organism is quite different from that expected from skeletal muscle (Fig. 6) (T. Roberts and R. Marsh, unpublished observations; Marsh and John-Alder, 1994). During the jump, velocity and force increase simultaneously for most of the take-off, whereas one would expect muscle force to be inversely related to shortening velocity, following the force–velocity relationship. The increasing force and velocity during take-off lead to a peak in power output late in the jump. How can the muscles produce this pattern of movement given their properties? This question has been approached using a combination of modeling and measurements of muscle function (Olson and Marsh, 1998; T. Roberts and R. Marsh, unpublished results).

The main job of the muscles powering the jump is to accelerate the mass of the frog to a take-off velocity that will determine the jumping distance. Studies in the past have realized the importance of the interaction between inertia and the properties of the muscle (Calow and Alexander, 1973; Lutz and Rome, 1996b; Marsh, 1990). However, this interaction was modeled without considering gravity or incorporating the elastic elements that are particularly important to jumping performance. The other morphological feature that is likely to be particularly important is a changing mechanical advantage

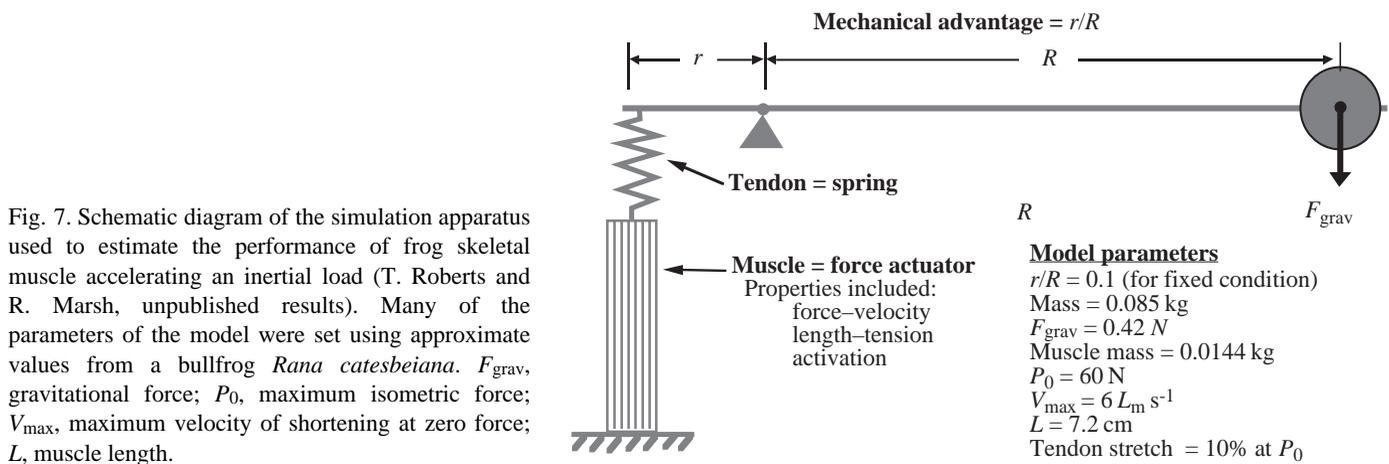


Fig. 7. Schematic diagram of the simulation apparatus used to estimate the performance of frog skeletal muscle accelerating an inertial load (T. Roberts and R. Marsh, unpublished results). Many of the parameters of the model were set using approximate values from a bullfrog *Rana catesbeiana*.  $F_{\text{grav}}$ , gravitational force;  $P_0$ , maximum isometric force;  $V_{\text{max}}$ , maximum velocity of shortening at zero force;  $L$ , muscle length.

due to the unfolding limbs. We hypothesized that a poor mechanical advantage early in the jump would allow the storage of elastic energy and the development of a high force in the activating muscles (T. Roberts and R. Marsh, unpublished results). We tested these ideas using a very simple model of a muscle attached to a mass *via* a mass-less lever (Fig. 7). The initial parameters of this model were set approximately to the values for an average-sized bullfrog *Rana catesbeiana*, a species that we have used to measure muscle function *in vivo*. The model was run for three conditions: (1) the muscle attached to the lever with a constant mechanical advantage and no elastic element; (2) the muscle attached to the lever with a constant mechanical advantage and containing an elastic element in series; and (3) the muscle attached *via* an elastic element to a lever whose mechanical advantage improved during the movement.

The three conditions differed greatly in their predicted mechanical outputs. When the muscle moves the load *via* a simple lever with no elastic element, the pattern of change in velocity, force and power output is totally unlike that during jumping (Fig. 8A). The reason for this is obviously the mismatch between the requirements of the load and the basic properties of the muscle. As the load accelerates, force drops because of the force-velocity characteristics of the muscle. Adding an elastic element improves the match between predicted and measured outputs, and including an improving mechanical advantage gives a pattern of changing velocity, force and power most similar to that seen in a jumping frog (Fig. 8B). Under these last conditions, peak power exceeds that produced by the muscle because a portion of the power late in the contraction is derived from the recoiling elastic elements.

This simple model may be used to predict the length and velocity trajectories expected for a muscle accelerating an inertial load. Under the conditions of a changing mechanical advantage and in the presence of an elastic element, the muscle is predicted to shorten rapidly at first, to slow down and finally to accelerate as the elastic element recoils. Published records of length change in the muscles of jumping frogs do not correspond to this pattern (Lutz and Rome, 1994, 1996a; Olson and Marsh, 1998), but the muscles examined were parallel-

fibred thigh muscles. We examined the shortening and activation of the plantaris muscle of the bullfrog, which is a pinnate muscle with a long tendon (T. Roberts and R. Marsh, unpublished results). The length and velocity trajectories of this muscle during the jump correspond with those predicted from the model.

#### *Producing force to tension elastic elements*

During walking and running, muscles are required to do

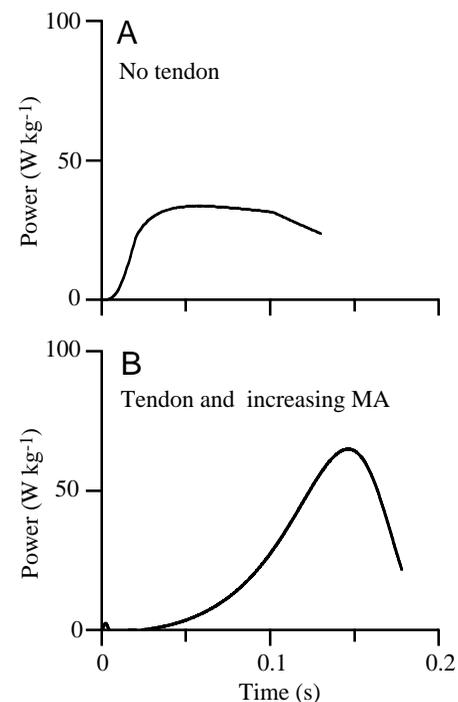


Fig. 8. Representative results from simulations of frog skeletal muscle accelerating an inertial load (T. Roberts and R. Marsh, unpublished results). Power output (per kilogram of mass accelerated) was calculated at the point where the mass contacts the lever. (A) Simulation with no elasticity or change in mechanical advantage. (B) Simulation with a series elastic element and a changing mechanical advantage (MA).

work when moving uphill and when accelerating (Roberts et al., 1997), but whether the production of mechanical work is important during level walking and running at a steady speed is not clear. Theoretical considerations and empirical data suggest that, during running, many muscles may function mainly to produce force. Investigations of the energetics of running have suggested that the primary energy-consuming process is force production to support the body weight of the running animal (Taylor et al., 1980; Kram and Taylor, 1990). Theoretical predictions based on the force–velocity curve of striated muscle suggest that muscles will produce force most economically when operating isometrically. Supporting this theory, recent investigations (Roberts et al., 1997; Biewener et al., 1998b) have found that the ankle extensor muscles of running and hopping animals primarily produce force during level locomotion. When forces are high during ground contact, these muscles operate nearly isometrically, providing the tension that allows effective storage of elastic energy. Recent work on running dogs is also consistent with the idea that the muscle/tendon units of the lower leg function mainly to store energy elastically during level running (Gregerson et al., 1998). This storage of elastic energy allows economical locomotion because most of the energy required to lift the center of mass in each stride can come from stored energy instead of from muscle work. In contrast, some work on cats has suggested that the ankle extensors do substantial amounts of net positive work during walking and running at relatively low speeds (Whiting et al., 1984; Prilutsky et al., 1996). This apparent difference in the function of cat ankle extensors may be due to species differences or to technical differences among the studies.

Also in need of further investigation are the roles of the thigh muscles in producing work during running. Deductions based on architectural properties have suggested that the long strap-like muscles of the thigh would be well suited to performing work during rapid movements. However, the only parallel-fibered muscle so far investigated using sonomicrometry, the posterior iliotibialis in birds, reveals a muscle that probably absorbs more work than it produces (see below). Investigations of two pinnate muscles in the thigh of running dogs have yielded ambiguous results because of variation among the animals tested (Carrier et al., 1998; Gregerson et al., 1998).

#### *Producing stability*

Muscles may play an important role in stability during locomotion, but our information on this potentially important function is limited. Students of human biomechanics have identified muscles that play stabilizing roles in slow movements such as standing up from a sitting position (Oddsson and Thorstensson, 1987) and balancing (Ivanenko et al., 1997), but have not in general approached questions of stability during rapid running.

The importance of stability can be brought into sharp focus when viewing the efforts of engineers trying to build legged robots. Many such efforts have resulted in statically stable slowly moving robots (Cruse et al., 1995). (Static stability

occurs when the center of mass is located above an area bounded by three or more support legs.) Dynamic stability has been built into some running legged robots (Raibert, 1991; <http://www.ai.mit.edu/projects/leglab/>) but, Hollywood fantasies aside, no one has yet made a robot that comes close to producing the rapid and stable locomotion of legged animals.

Stability may arise either from neural feedback loops that alter motor recruitment or from the properties of the locomotor system itself. Stabilizing properties of the peripheral system have the advantage of speed of response and may be particularly important during rapid movements. The potential for the intrinsic properties of muscle to stabilize rates of movement has been pointed out many times (e.g. Grillner, 1972; Hogan, 1990; Marsh, 1990; van Soest and Bobbert, 1993; Brown et al., 1995).

We know little about how individual muscles help to produce stability and whether particular length trajectories are involved. Past discussions have emphasized muscle co-contraction as a way to control joint stiffness and thus produce stability (Hogan, 1990). In this role, co-activation of muscles has been seen as a way to maintain joint position or to perform precise slow movements. Co-contraction of muscles during large joint excursions will cause active lengthening ('eccentric contraction') of the muscles that oppose the movement. This active lengthening will absorb energy, reduce economy (Hogan, 1990) and has the potential to produce damage (Stauber, 1989). For these reasons, one might expect that co-contraction would be kept to a minimum when excursions are large. However, natural selection has undoubtedly acted strongly to maintain stability as well as economy, and it is fair to ask whether there have been trade-offs between the two.

Recent investigations have found muscles that apparently absorb large amounts of work during running. Full et al. (1998) have suggested that one of the extensor muscles in the cockroach helps to stabilize rapid running. This muscle undergoes substantial strain during running, but appears to absorb more work than it produces. The hypothesis that this muscle promotes stability was arrived at by exclusion. Its length trajectory and activity simply do not fit with other possible functions during running. It neither acts isometrically to produce force nor shortens to do net work.

Similar reasoning has led to the hypothesis that the posterior iliotibialis muscle in running birds also functions primarily to produce stability (C. Buchanan and R. Marsh, unpublished observations). This muscle undergoes a substantial strain during running and lengthens by approximately 15% while it is fully active as measured by electromyography (Fig. 9). The peak rate of lengthening is very high, up to  $6 \text{ lengths s}^{-1}$ . This bi-articular muscle is both a knee extensor and a hip extensor, but measurements of the excursion at these joints indicate that active stretch is due to knee flexion. Given the anatomical location of the iliotibialis, one might expect that ground reaction forces would drive this lengthening. However, in running birds, the ground reaction vector is initially in front of the knee, leading to an extensor moment at the knee during the

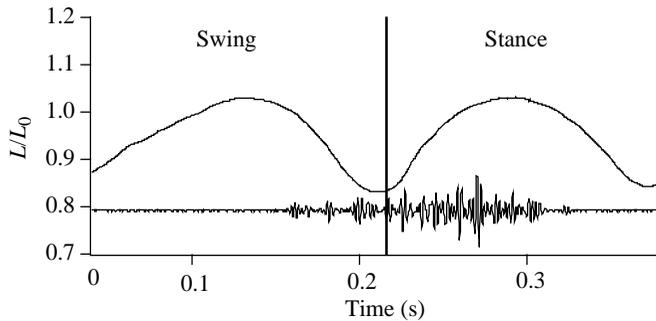


Fig. 9. Length and electromyographic activity of the posterior iliotibialis muscle in a guinea fowl *Numida meleagris* running at  $2.0 \text{ m s}^{-1}$  (C. Buchanan and R. Marsh, unpublished).  $L$ , muscle length;  $L_0$ , muscle length at which isometric force is maximal.

first part of contact (T. Roberts, personal communication). Knee flexure, which stretches the iliotibialis, during early contact has to be produced actively by knee flexors, a number of which show activity simultaneous with the iliotibialis (Gatesy, 1999). To flex the knee, the flexors must not only oppose the ground reaction force but also work against the active iliotibialis muscle.

Unfortunately, we do not know enough about muscle function under the conditions found for the iliotibialis muscle to model its behavior. The amount and rate of lengthening of this muscle are unprecedented, and no *in vitro* data are available for any muscle under similar conditions. These kinds of results emphasize the importance of knowing what muscles actually do during natural movements when designing *in vitro* contractile studies.

The discovery that major muscles may be involved in producing stability raises important questions. Do co-contracting sets of muscles function particularly well in producing stability? How much of the energy used during running is spent on stabilization? Do differently designed animals differ in the amount of energy required to stabilize running?

I would like to thank John Altringham for inviting me to participate in the symposium honoring R. McNeil Alexander from which this contribution stemmed. To Brian Clark goes the credit for first calling to my attention to the work of Alexander when I was a graduate student. This work was a key to the realization that the mechanical function of muscles *in vivo* could be a fruitful line of investigation.

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