DISSECTING MUSCLE POWER OUTPUT

ROBERT K. JOSEPHSON*

School of Biological Sciences, University of California, Irvine, CA 92697, USA

*e-mail: rkjoseph@uci.edu

Summary

The primary determinants of muscle force throughout a shortening–lengthening cycle, and therefore of the net work done during the cycle, are (1) the shortening or lengthening velocity of the muscle and the force–velocity relationship for the muscle, (2) muscle length and the length–tension relationship for the muscle, and (3) the pattern of stimulation and the time course of muscle activation following stimulation. In addition to these primary factors, there are what are termed secondary determinants of force and work output, which arise from interactions between the primary determinants. The secondary determinants are length-dependent changes in the kinetics of muscle activation, and shortening deactivation, the extent of which depends on the work that has been done during the preceding shortening. The primary and secondary determinants of muscle force and work are illustrated with examples drawn from studies of crustacean muscles.

Key words: muscle, work, power, shortening velocity, *Carcinus maenas*.

Introduction

In 1977, Weis-Fogh and Alexander published a theoretical study of the sustained mechanical power available from skeletal muscle, a study that was very influential in shaping my own thinking about muscle. Earlier considerations of muscle power had emphasized the instantaneous power output, obtained from force–velocity plots as the product of force and the associated shortening velocity (see Fig. 3), but not the power output over a complete contraction–relaxation cycle. The approach used by Weis-Fogh and Alexander (1977), and in a conceptually similar study by Pennycuick and Rezende (1984), was to evaluate the work done as the integral of force times increment of length change:

$$W = \int F \mathrm{d}L, \qquad (1)$$

where W is work output, F is muscle force and L is muscle length. This integral, evaluated over a full cycle, is the work done per cycle; the product of work per cycle times cycle frequency is the power output. If force is expressed as stress (=force/cross-sectional area) and length change as strain ($=\Delta L/L$), their product is work per muscle volume [≈work/mass, exactly equal to (work×muscle density)/mass], and the rate at which work is done is power/volume (≈power/mass). For a given length change, the factors that determine the instantaneous value of muscle force are those that determine the work output. The determinants of muscle force during a contraction are summarized in Fig. 1. These may be divided into primary determinants and secondary determinants, the latter resulting from interactions between the primary factors. The primary determinants are the instantaneous muscle length (the length–tension relationship), the shortening or lengthening velocity (the force–velocity relationship) and the degree of muscle activation, which reflects when and in what pattern the muscle was stimulated and the time course of the rise and fall of activation following stimulation. The secondary determinants are the effects of muscle length on the time course of muscle activation, and deactivation associated with shortening and work production. It is a deactivation, which occurs with a small delay following shortening, and its lengthening counterpart, delayed activation following stretch, that allow asynchronous flight muscles of insects to contract in an oscillatory fashion when attached to an appropriate, resonant load (for a review, see Pringle, 1978). Unfortunately, little is known about the determinants of force and work during the oscillatory contraction of asynchronous muscles, and asynchronous muscles will not be considered further here. Finally, the force generated by the cross-bridges (contractile components, CC) are connected to the load by compliant linkages (the series elastic component, SEC) whose properties can affect the length and velocity of the contractile elements and therefore work output.

The following review examines in somewhat greater detail those factors that affect force and therefore power output during cyclic contraction of muscle.

Power output during cyclic muscle contraction

The muscles

The muscles chosen to illustrate concepts are two crustacean muscles, the flagellum abductor (FA) and a respiratory muscle,
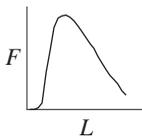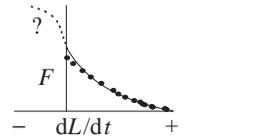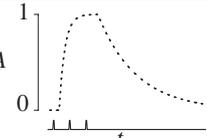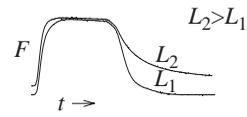
Primary determinants	
A Force (F) f length (L)	
B F f dL/dt	
C Activation (A) f time (t)	
Secondary determinants	
D A f L	
E A f work (W)	
Coupling to load	
F $L = L_{CC} + L_{SEC}$ L_{SEC} f F	
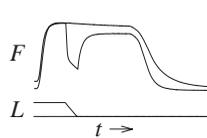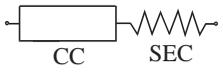
Fig. 1. The determinants of force, and therefore of work output (W), during muscle shortening or lengthening. The figures in the right column are as follows. (A) Maximum isometric force (F) as a function (f) of muscle length (L) (crab flagellum abductor muscle). (B) Muscle force during tetanic stimulation as a function of shortening velocity, dL/dt (crab flagellum abductor muscle), where t is time. The lengthening portion of the curve has the shape often assumed to be appropriate for muscle, but is drawn with a dotted line to indicate the inexactitude of this relationship. (C) The time course of muscle activation (A), drawn with a dotted line to indicate that this curve is largely imaginary without firm experimental foundation. (D) Force during isometric, tetanic contraction at two lengths (crab scaphognathite levator muscle L2B). Note the slower relaxation rate at the longer muscle length. (E) Force during tetanic contractions with and without a ramp release to a shorter length (crab scaphognathite levator muscle L2B). The force re-developed following release is depressed relative to that in the isometric contraction. (F) The commonly accepted view of muscle as consisting of a contractile component (CC) and a series elastic component (SEC).

scaphognathite levator muscle L2B, from the green crab *Carcinus maenas*. Information on the innervation pattern, ultrastructure and contractile properties of these muscles can be found in Josephson and Stokes (1987, 1994) and Stokes and Josephson (1992). These crustacean muscles were selected as examples not because they are unusual in any obvious way, but because I have worked with them and they are the muscles with which I am most familiar. In fact, in their mechanical properties during tetanic stimulation, the FA and muscle L2B are quite like more commonly studied frog and mammalian muscles.

Length–tension relationships

It has long been known that there is an optimum muscle length for force production. Since the classic work of Gordon et al. (1966), the decline in force with stretch beyond the optimum length has been attributed to a reduction in the amount of overlap between thick and thin filaments and therefore a decrease in the number of potentially active cross-bridges. The reduction in force with shortening below the optimum length is thought to be due to hindrance between thin filaments when these meet in the middle of the sarcomere, to overlap between thin filaments and cross-bridges of inappropriate polarity when the thin filaments slide beyond the middle of the sarcomere and to compressive forces produced when the thick filaments reach the Z-line.

The study of length–tension relationships by Gordon et al. (1966) was performed with isolated segments along single muscle fibers. Sarcomeres within a short fiber segment were expected to be of similar length and filament overlap. The resulting length–tension diagram was made up of a series of linear segments. This diagram has now become commonplace in all modern texts dealing with muscle contraction. However, in real muscle, the length–tension curve is more bell-shaped than polygonal (Fig. 2). The deviation between the length–tension
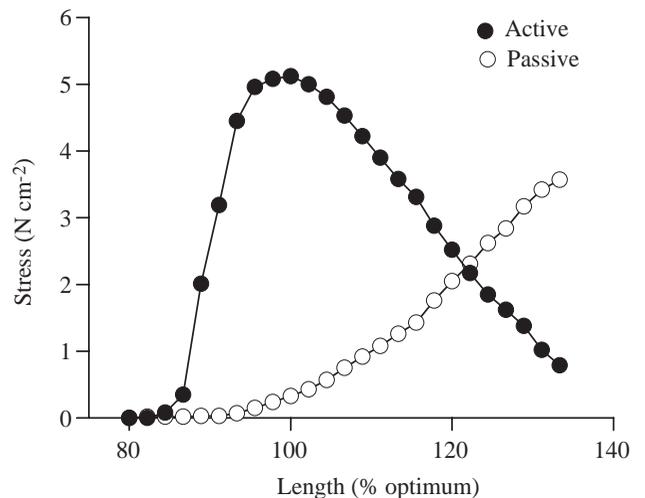
Fig. 2. Muscle length and muscle force (crab flagellum abductor muscle). The open symbols are the stress in the unstimulated muscle at different muscle lengths; the filled symbols are the increase in stress above the passive level evoked by maximal tetanic stimulation. Original data from Stokes and Josephson (1994).

Fig. 3. Force–velocity relationship (crab flagellum abductor muscle). (A) The experimental procedure used. The muscle was stimulated tetanically and allowed to develop tension at constant length. In three of the four trials shown, the muscle was released at the arrow to isotonic shortening at a selected load. The lower set of traces is the course of muscle shortening during the load clamp. The initial slope of these traces is taken as the strain rate (muscle lengths per second, $L\,s^{-1}$) at the relevant load. (B) The filled symbols are the initial strain rates measured at a number of different loads. The line joining the symbols is a Hill curve (see text). The dotted line is the instantaneous power output, obtained as the product of stress and strain rate. Original data from Stokes and Josephson (1994).
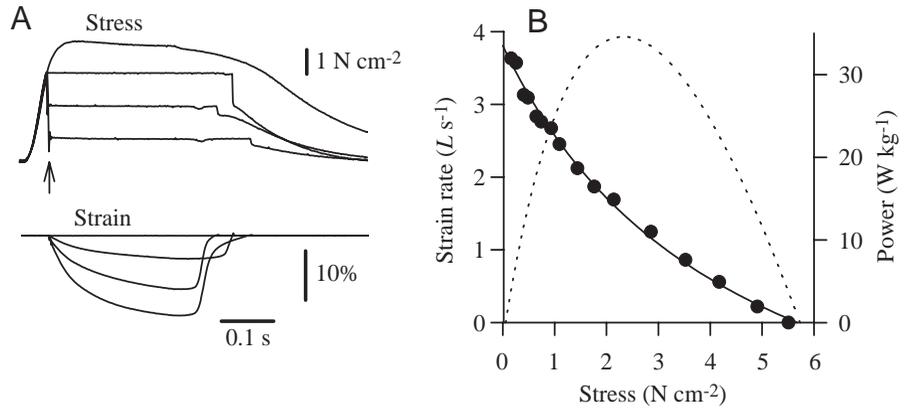
behavior expected from the Gordon–Huxley–Julian model and that of whole muscles presumably results from inhomogeneities among the sarcomeres of whole muscles and possibly from inhomogeneities in the lengths of thick and thin filaments in individual sarcomeres (Edman and Reggiani, 1987). If either sarcomeres or filaments are not all of similar length, there will be dispersion in the values of overall muscle length at which individual thin filaments during shortening first reach the central bare zone of a sarcomere, at which they begin to overlap with thin filaments from the opposing Z-line or at which they encounter oppositely oriented cross-bridges, dispersion that will result in gradual rather than sharp transitions at critical points along the length–tension curve.

Force–velocity relationship

There is an inverse relationship between the force on a muscle and the velocity with which it can shorten (Fig. 3). The force–velocity relationships of muscles or muscle fibers are commonly fitted to the hyperbolic relationship of Hill (1938):

$$(F+a)(V+b)=(F_0+a)b=\text{constant}. \tag{2}$$

where F is force, V is velocity, F_0 is maximum isometric force and a and b are constants. Alternative functions that fit the experimental points better, especially those at very high and very low velocities, have been proposed (Marsh and Bennett, 1986; Edman, 1988), but these require more than the two fitting constants of the Hill equation. In tetanically stimulated frog muscle fibers, operating near the plateau of the length–tension curve, muscle force is reasonably constant during isovelocity shortening, and the velocity is reasonably constant during isotonic shortening. In many muscles, however, force declines during the course of isovelocity shortening, and shortening velocity declines during isotonic contraction (Fig. 3). These changes in force or velocity have been attributed to shortening deactivation (Floyd and Smith, 1971; see below). When force or velocity changes during a contraction, it is customary to use the early values of force or velocity, those shortly after the transition to isovelocity or isotonic contraction, to construct force–velocity curves.

In most behaviors involving cyclic muscle activity, the participating muscles spend about as much time lengthening as they do shortening. There is an abundance of data on the force–velocity properties of shortening muscle but a paucity of such information for lengthening muscles. Several force–velocity curves for lengthening muscle have been published (see, for examples, Fig. 2.21 in Woledge et al., 1985). However, in most relevant studies, there is not a single-valued relationship between force and lengthening velocity. Rather, muscle force rises continuously during isovelocity stretch, and velocity changes continuously during isotonic lengthening (Fig. 4; literature surveyed in Josephson and Stokes, 1999a). A common pattern among skeletal muscle is for force to rise continuously but at a declining rate during stretch at low velocity and to rise to a yield point during high-velocity stretch, following which force may continue to rise but at a lower slope, or be reasonably constant, or sometimes fall even though stretch is continued (see, for example, Sugi and Tsuchiya, 1988; Malamud et al., 1996; Sandercock and Heckman, 1997). At the end of stretch, force declines gradually and can remain above the isometric level expected at the stretched length for many seconds (see Edman and Tsuchiya, 1996, and references therein). The enhanced force following stretch is probably due in part to the increased heterogeneity in sarcomere length along a fiber that develops during the stretch (Edman and Tsuchiya, 1996). Since force varies continually during isovelocity stretch, to predict the force in a lengthening muscle requires knowledge of the time since the onset of stretch as well as the stretch velocity. The force–velocity relationship of lengthening muscle is not a planar curve; rather, it is a surface with time of stretch as a third axis (Fig. 5).

Time course of activation

The capacity of a muscle to generate force and do work rises rapidly following stimulation and then falls during relaxation. Despite its obvious importance and the many studies devoted to it, the development of an appropriate

Fig. 4. Force during isovelocity stretch (crab scaphognathite levator muscle L2B). The pre-stretch and post-stretch lengths were chosen such that the isometric force at the two was approximately equal, as is shown by the force developed in the trace in which the stretch came well before the onset of stimulation (stimulation is marked by the line below the force traces). The small arrow indicates relaxation in the trial in which stretch preceded stimulation. The relaxation rate at the longer, stretched muscle length is slower than that at the shorter, control length without stretch. (B) An expanded view of the portion of A during which there was stretch of the active muscle. Note that stress changes continuously during stretch (from Josephson and Stokes, 1999a).
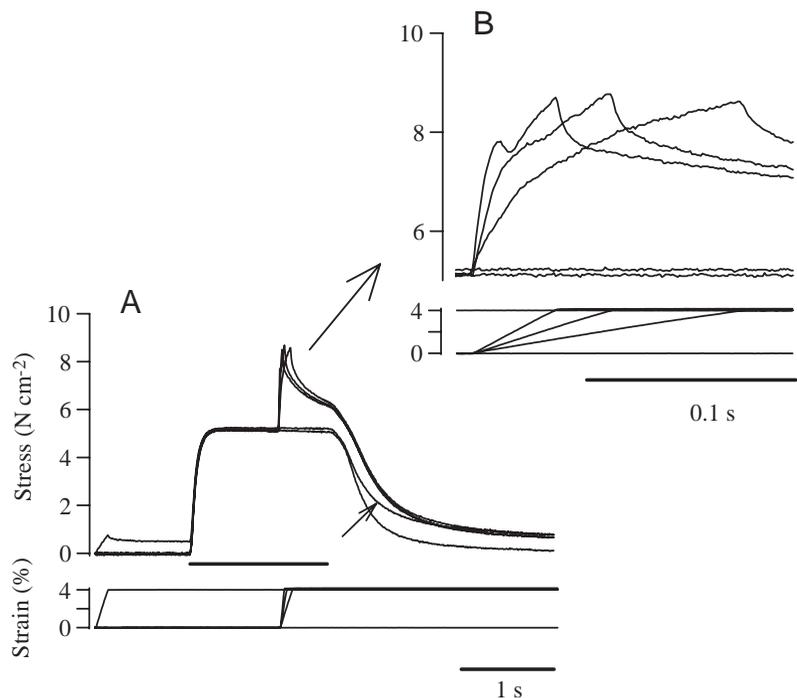
measure of muscle activation which might be used to quantify the changing capacity of a muscle to develop force and to do work following stimulation has been an elusive goal (for a review, see Ford, 1991). Techniques have been developed for measuring variation in cytoplasmic Ca^{2+} concentration and in instantaneous stiffness of muscle associated with activation, but Ca^{2+} concentration and stiffness are only indirectly related to the capacity to generate force and to do work. Some measure of the changing position and possibly shape of force–velocity curves following stimulation is needed, but what this measure might be is not obvious. Ford (1991) suggests using maximum power, determined from force–velocity curves, as a measure of muscle activation. But to reach the force at which power is maximal early in a contraction requires stretching the muscle and introduces the possibility of stretch activation as well as the complexities in the force–velocity relationship associated with stretch described above. The many early studies on the time course of the 'active state' in frog muscle suggest that activation rises abruptly and decays exponentially following a short plateau (e.g. Hill, 1949; Jewell and Wilkie, 1960). We used the shortening velocity at a fixed, light load to characterize activation during the twitch of a locust flight muscle (Malamud and Josephson, 1991) and concluded that, here too, activation following stimulation rose rapidly to a maximum, reached 2–3 ms after the end latent period, and then, after a brief plateau, decayed approximately exponentially. The general shape of the activation *versus* time curve in the locust muscle was similar to that in frog muscle but on a faster time scale. This pattern, a rapid rise followed by exponential decay, may be the common one among skeletal muscles.
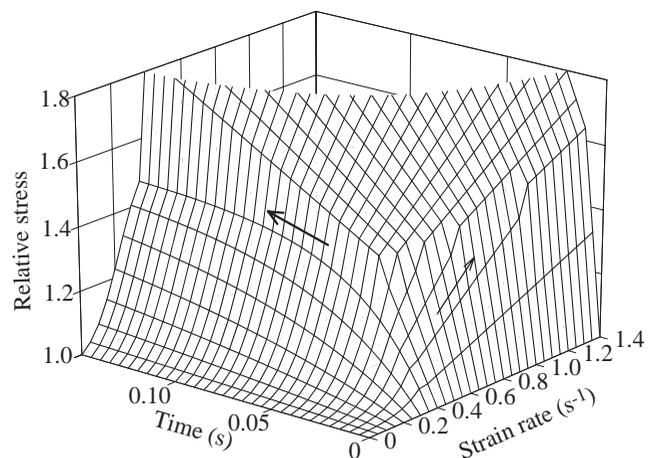

Fig. 5. The stress–strain rate–time surface for crab scaphognathite levator muscle L2B during lengthening. Relative stress is stress relative to the isometric stress preceding stretch. The trajectory along a strain rate isogram, such as that shown by the thicker arrow, is the change in stress as a function of time during stretch. The trajectory along a time isogram, such as that shown by the thinner arrow, is the stress–strain rate relationship at a given time after the onset of stretch.

Activation and muscle length

It seems to be a general feature of muscle that relaxation becomes slower as muscle length increases (e.g. Hartree and Hill, 1921; Close, 1972; Malamud, 1989; see also Fig. 4). The increase in relaxation time has been attributed to an increase in the Ca^{2+} affinity of myofilaments with increasing muscle length (Stephenson and Wendt, 1984). In intact organisms, an increase in contractile duration with increase in muscle length
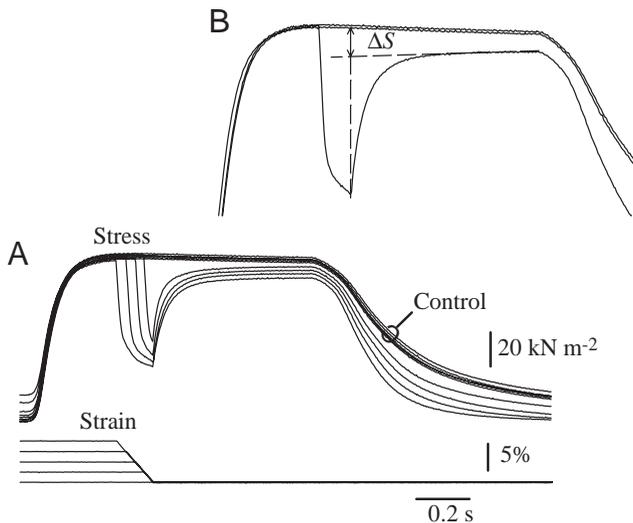
Fig. 6. Depression of the force redeveloped following isovelocity shortening for varied distances (crab scaphognathite levator muscle L2B) (from Josephson and Stokes, 1999b). The difference between the force redeveloped following shortening and the control force increases with increasing distance of shortening. (B) The method used to measure deactivation. It is assumed that the recovery of force following shortening has two components; an initial, rapid force rise, with a time course rather like that at the onset of contraction, and a later, slow force increase representing decay of the depression due to the shortening. Extrapolation of the latter part of the force recording back to the end of shortening is used to determine ΔS, which is proposed to be the extent of deactivation at the end of shortening.

should partially compensate for the decline in force as a muscle is stretched into the descending limb of the length–tension curve. If a muscle becomes stretched because of load or increased activity in antagonistic muscles, its contractions become longer and the time-average of its force becomes greater than would be the case were activation not length-dependent.

Work-dependent deactivation

Another feature modifying muscle force, which appears to be common among skeletal muscles, is a depression of the capacity to develop tension following active shortening. In frog muscle fibers (Granzier and Pollack, 1989) and in crab muscles (Josephson and Stokes, 1999b), the extent of the depression increases with increasing distance of shortening (Fig. 6) and is inversely related to the velocity of shortening (Fig. 7). The reduced capacity to develop force following shortening is frequently described as 'shortening deactivation'. However, it is not simply the amount of shortening that determines the degree of depression, since the latter also varies with the velocity of shortening and therefore with the force during shortening and the work done. Granzier and Pollack (1989) found that in frog muscle the magnitude of force depression following shortening is closely correlated with the work done during shortening, and the same is true in crab muscle (Fig. 8). Hence, the deactivation associated
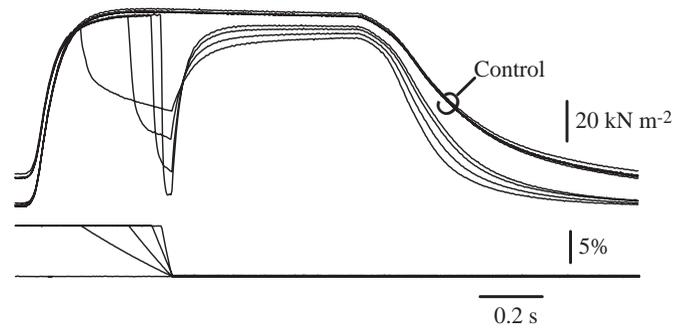

Fig. 7. Depression of force redevelopment following isovelocity shortening at different strain rates (crab scaphognathite levator muscle L2B). The slower the strain rate (and the greater the force during shortening), the greater the depression of force following shortening.
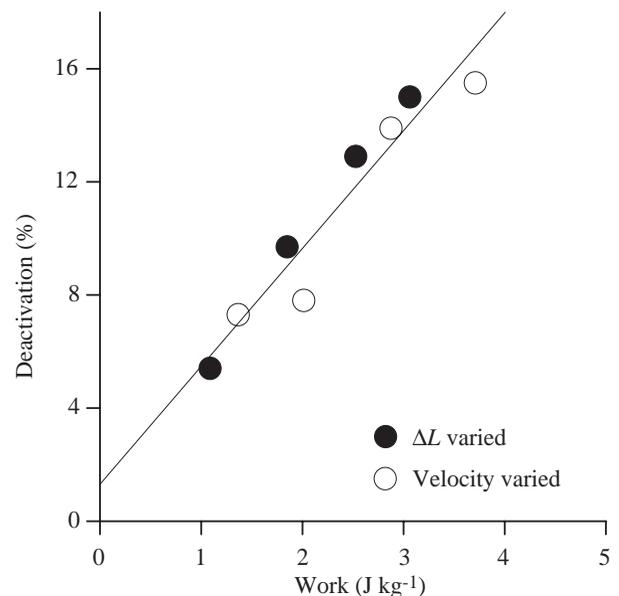

Fig. 8. The relationship between force depression following shortening, measured as in Fig. 6, and the work done during shortening. The filled symbols are from trials such as that of Fig. 6 in which the strain rate was constant and the distance (ΔL) varied; the open symbols from trials such as those of Fig. 7 in which shortening distance was constant and strain rate varied. The equation for the line is: $y=4.2x+1.3$, $r^2=0.92$, $P<0.001$.

with shortening is better described as 'work-dependent deactivation' than as 'shortening deactivation'.

Consequences of series elasticity

The force generated by cross-bridges is transmitted to the load through myofilaments, Z-lines and tendons or apodemes, all of which are to some extent compliant. The compliant elements interposed between the force generators and the load are described collectively as the series elastic component (SEC). Stretch of the SEC is generally found to be a non-linear function of stress. The presence of series elasticity allows some internal sliding of filaments and shortening of sarcomeres when

the muscle as a whole is held at constant length in an 'isometric' contraction. Length changes in the SEC are in series with and additive to those of the contractile elements. The length change and velocity of the contractile component may be greater than or less than that of the muscle as a whole depending on whether force is rising and the SEC is becoming stretched or force is falling and the SEC is shortening. Force–velocity relationships for the contractile component derived from isotonic contractions in which force and SEC length are constant will not apply exactly to the usual conditions of muscle use *in vivo* during which force changes continuously and, therefore, so does SEC length. The consequences of series elasticity on work and power output of muscle are well illustrated in a recent paper by Curtin et al. (1998).

Synthesizing muscle models

The factors listed in Fig. 1, and perhaps others yet to be discovered, determine the work output during length change. These, then, are the elements that might be included in a model of mechanical power production by muscle. Some may be quantitatively insignificant in particular cases, but it seems prudent to consider them all if postulated models of muscle power are to be accurate reflections of real muscle performance. Some of the components of Fig. 1 are well-studied, in particular force–velocity relationships and length–tension relationships, the others less so. But being well-studied is not the same as being well-understood. The length–tension relationship in small muscle segments may not show a sharp transition between a plateau and the descending limb, even though theory predicts it should (Edman and Reggiani, 1987). Force–velocity relationships may have an odd and unexplained concavity at the high-force end (Edman, 1988). But, in general, the determinants of force and work output seem sufficiently if not exactly understood that they could be included in a model of work output.

Several recent studies have examined the extent to which the force during muscle stimulation and movement patterns simulating those of normal activity can be predicted from the force–velocity and length–tension properties of the muscle and usually a postulated time course for the state of muscle activation (Caiozzo and Baldwin, 1997; Sandercock and Heckman, 1997; Askew and Marsh, 1998; Curtin et al., 1998; Williams et al., 1998). In general, the predicted force matched measured force reasonably well early in contractions, but there tended to be deviation late in a cycle, especially during relaxation following shortening. None of the studies directly incorporated work-dependent deactivation, realistic views of the force–velocity relationships during muscle lengthening or enhanced force following lengthening, although the paper by Askew and Marsh (1998) did calculate the time course of activation in general as the ratio between the muscle force actually measured and that expected from muscle velocity and length. I think it highly likely that incorporating work-dependent deactivation and more accurate representations of the force–velocity properties of lengthening muscle would substantially improve the theoretical muscle models as predictors of real muscle behavior. The early study of Weis-Fogh and Alexander (1977) provided a framework for considering the potential work output of muscle; the task now is to add and shape details so as to make the structure increasingly realistic.

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