The integrated function of muscles and tendons during locomotion☆

Thomas J. Roberts*

Oregon State University, Department of Zoology, 3029 Cordley Hall, Corvallis, OR 97331-2914, USA

Abstract

The mechanical roles of tendon and muscle contractile elements during locomotion are often considered independently, but functionally they are tightly integrated. Tendons can enhance muscle performance for a wide range of locomotor activities because muscle–tendon units shorten and lengthen at velocities that would be mechanically unfavorable for muscle fibers functioning alone. During activities that require little net mechanical power output, such as steady-speed running, tendons reduce muscular work by storing and recovering cyclic changes in the mechanical energy of the body. Tendon stretch and recoil not only reduces muscular work, but also allows muscle fibers to operate nearly isometrically, where, due to the force–velocity relation, skeletal muscle fibers develop high forces. Elastic energy storage and recovery in tendons may also provide a key mechanism to enable individual muscles to alter their mechanical function, from isometric force-producers during steady speed running to actively shortening power-producers during high-power activities like acceleration or uphill running. Evidence from studies of muscle contraction and limb dynamics in turkeys suggests that during running accelerations work is transferred directly from muscle to tendon as tendon stretch early in the step is powered by muscle shortening. The energy stored in the tendon is later released to help power the increase in energy of the body. These tendon length changes redistribute muscle power, enabling contractile elements to shorten at relatively constant velocities and power outputs, independent of the pattern of flexion/extension at a joint. Tendon elastic energy storage and recovery extends the functional range of muscles by uncoupling the pattern of muscle fiber shortening from the pattern of movement of the body.
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1. Introduction

Considerable progress has been made in recent years in our understanding of how the mechanical properties of muscles determine the energetics and mechanics of animal movement. A detailed under-

standing of the physiological basis for force production in muscle contractile elements—including contractile properties like the force–velocity relationship, length-tension relationship, and the dynamics of muscle activation—make it possible to test predictions about how muscles should operate in vivo in order to maximize performance. Various experimental approaches have demonstrated that the patterns of shortening that muscles undergo during natural movements are well matched to their contractile properties (Lutz and Rome, 1994; Marsh and Olson, 1994; Askew and

Marsh, 1997; Wakeling and Johnston, 1998). The observation that muscle contractile elements experience favorable loads and operate at favorable velocities during ordinary movements suggests that muscle contractile properties are well matched to elements of the musculoskeletal system such as lever systems, elastic elements and body and segment masses.

Our improving understanding of muscle function in vivo prompts new questions about the mechanical role of tendons during locomotion. It is well known that mechanical energy storage and recovery in tendons is an important energy-conserving mechanism during some forms of locomotion, such as running (Cavagna et al., 1964; Alexander, 1984, 1988). However, the mechanism of elastic energy storage and recovery is usually considered independently of the mechanism of active force and work production. Here I examine the function of tendons during running in the context of muscle contractile properties. Evidence from a range of studies indicates that tendon elasticity can have a decisive influence on the pattern of length changes that muscles undergo during movement. Tendon length changes provide advantages during locomotion that are only apparent in light of their direct interaction with muscle contractile properties. The mechanical abilities of muscle–tendon units as integrated actuators far exceed the capabilities of muscle contractile elements alone.

2. Compliance of tendons

Tendon's dynamic function is determined by its elastic behavior; it changes length in proportion to the applied load. This property is not unique to tendon; many structures in muscle are compliant enough to undergo significant length changes under typical muscular loads. Historically, muscle compliance has been divided according to where the compliance acts in relation to the force-producing component of muscle (Hill, 1938). Series elasticity operates in series with the force-producing component; length changes in the series elastic component and the force-producing component are additive. Parallel elasticity operates in parallel with the force-producing component; forces in the parallel elastic component and the force-producing component are additive. The structures responsible for the parallel elastic component of muscle include connective tissue binding muscle fibers and fascicles together, as well as intrafibrillar

proteins such as the large molecular spring titin (Magid and Law, 1985; Wang et al., 1993; Kellermayer et al., 1997). These structures typically also exhibit significant viscosity in addition to their elastic behavior. Tendon is of course a series elastic structure, but series elasticity also resides within cross-bridges themselves, actin filaments, and to a lesser degree myosin filaments (Linari et al., 1998). A quick, short stretch of an active muscle will result in an increase in force that is a result of the elastic stretch of tendon, bound cross-bridges and motor protein filaments. Thus, the changes in length that muscles undergo due to action of the contractile component (that is, the active development of force by cross-bridge cycling) is affected by both tendon as well as other components of series elasticity.

Despite the potentially complicated interaction of the many elastic structures within muscle, the relative importance of tendon compliance can be illustrated with a simple experiment. In a 'fixed-end contraction', the entire muscle–tendon unit is held at a constant length while the muscle is stimulated to produce maximal tetanic force (e.g. Lieber and Boakes, 1988; Griffiths, 1991). If muscle fascicle length is independently measured during the contraction, shortening of muscle fibers can be observed. Because the muscle–tendon unit length is held constant, the shortening of the muscle fascicles is possible only with the stretch of the series elastic component external to the muscle fascicles, i.e. the tendon. Muscle fascicle shortening in a fixed-end contraction is a measure of tendon lengthening, and therefore can be used along with muscle force to calculate tendon compliance. Fig. 1 illustrates the use of sonomicrometric measurements of muscle fascicle length in a fixed-end contraction to provide a measure of tendon compliance. In this example of a contraction in a turkey lateral gastrocnemius, the muscle fascicles shorten by approximately 10% of their resting length against lengthening of the tendon.

Measurements of muscle contractile unit shortening in fixed-end contractions not only reliably isolate the tendinous component of muscle elasticity, they also provide a measure of tendon compliance that is a particularly convenient measure of the effect tendon length changes can have on contractile component length changes. Muscle fiber strain (the ratio of muscle length change to resting fiber length) from rest to peak tetanic force in a fixed-end contraction is dependent upon the
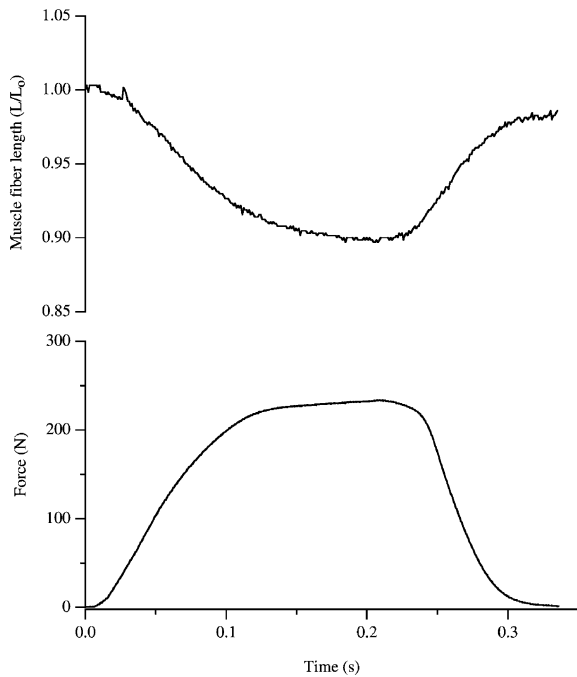
Fig. 1. Muscle force production and muscle fiber shortening in a fixed-end contraction in turkey lateral gastrocnemius. The intact muscle was stimulated with a bipolar nerve electrode, and the site of origin and insertion of the muscle were held immobile by a rigid frame. Muscle fiber length was measured by implanted sonomicrometer crystals, and force was measured by strain gages glued to bony tendon (Roberts et al., 1997). Muscle length is normalized to the starting length of the muscle during contraction.

compliance of the tendon, the force-generating capacity of the muscle, and muscle fiber length. The measure of muscle fiber strain in a maximal tetanic fixed-end contraction has been used widely by biomechanists and muscle physiologists; for convenience I will refer to it as the 'fixed-end compliance'. The fixed-end compliance is a particularly useful measure of tendon compliance for those interested in the mechanical function of muscle contractile elements during ordinary movements, because it expresses tendon compliance in terms of its potential influence on muscle fiber shortening. The fixed end compliance can be compared with the capacity for shortening of the muscle contractile components, typically assumed to be 30% or less of resting fiber length. A muscle with a fixed-end compliance of 30%, for example, will have a tendency to expend a large fraction of its shortening capacity on stretching tendon rather than causing skeletal movements. In muscles with high fixed-end compliance, the stretch and recoil

of elastic tendons can be more important than skeletal movements for determining the pattern of length changes in active muscle fibers.

Fixed-end compliance varies widely between muscles. Models of muscle contraction together with measures of tendon compliance have provided estimates of fixed-end compliance of frog semitendinosus and gastrocnemius of 11 and 21%, respectively (Lieber et al., 1991; Trestik and Lieber, 1993). In situ sonomicrometer measurements of muscle fiber length changes during shortening in fixed-end contractions measured fixed-end compliance of 28% in the cat lateral gastrocnemius (Griffiths, 1991) and 13% in the lateral gastrocnemius of guinea fowl (Buchanan and Marsh, 2001). Recent advances in ultrasound measurements of muscle and tendon dimensions in vivo have made it possible to determine fixed-end compliance during in vivo contractions. The gastrocnemius in humans shortens by 35% during maximal voluntary contractions with the origin and insertion of the muscle–tendon unit held stationary (Narici et al., 1996), and the tibialis anterior shortens by 23% [calculated from an estimated muscle fiber length of 70 mm (Maganaris and Baltzopoulos, 1999) and a tendon/aponeurosis length change of 16 mm, (Maganaris and Paul, 2000)]. By contrast, muscles with long fibers and small tendons can have very low fixed-end compliance. Early muscle physiologists chose frog sartorius for in vitro muscle experiments in part because its low compliance assured that muscle length changes measured in vitro were occurring primarily in the contractile elements and not in the series elastic elements (Hill, 1950).

What is the relative importance of the tendinous component of muscle elasticity compared with the other elasticity within the muscle? The degree of stretch that can be accommodated by the elastic behavior of the non-tendinous component of the series elasticity is limited by the distance actomyosin-cross bridges can be stretched before they are forcibly detached. Estimates of this value vary between studies, but it is generally accepted that the value of the 'short-range stiffness' is less than 12 nm per half sarcomere, or less than 2% of resting fiber length for vertebrate skeletal muscle (Huxley and Simmons, 1971; Getz et al., 1998). Thus, for muscles such as those discussed above, the fixed-end compliances of 11–35% suggest that the intrafibrillar component of series elasticity is likely to have an insignificant effect on muscle

length changes relative to the effect of the elastic behavior of tendon. Experiments that separate out the relative importance of tendon and non-tendon components of the series elasticity have demonstrated that tendon elasticity predominates in many muscles (Morgan, 1977; Ettema and Huijing, 1989, 1993). The limited range of extension of intrafibrillar compliant structures also translates into a very small capacity for energy storage within muscle compared with the energy storage capacity of tendon (Alexander and Bennet-Clark, 1977). Within muscles with short tendons and long fibers, such as the frog sartorius, the compliance of the non-tendinous component of the series elastic element may dominate the elastic behavior of the muscle (Bressler and Clinch, 1974).

Why are some muscle-tendon units compliant while others are relatively stiff? Most of the variation in fixed-end compliance between muscles results from differences in muscle and tendon architecture. Highly pennate, distal limb muscles typically have the highest values of fixed-end compliance. These muscles generate high forces, have relatively short fibers, and may have long and relatively thin free tendons in addition to the aponeurosis necessary in a pennate muscle. In a broad survey of mammalian limb muscles, Ker et al. (1988) used measurements of muscle and tendon dimensions to examine the variation in relative compliance between muscles. They defined a fiber-length factor, L, as the ratio of muscle fiber length to the extension of the tendon at peak tetanic tension, or the reciprocal of the fixed-end compliance (tendon extension was calculated assuming a peak muscle stress of 0.3 MPa and a tendon elastic modulus of 1500 MPa). Muscle compliance varied widely with muscle architecture. Some pennate muscles had fixed-end compliances greater than 50%, near or beyond the limit expected for maximal active muscle fiber strain (Ker et al., 1988). The majority of muscles in the survey had fixed-end compliances of less than 25%, though further distinctions within this grouping were not made. Ker and coworkers argued that variation in the relative compliance of tendons has been shaped by selective factors that operate to minimize muscle mass (Ker et al., 1988).

Though dimensional characteristics of tendons explain most of the variation in fixed-end compliance between different muscles, variation in material properties between tendons also has the potential to affect compliance. Evidence for significant, systematic variation in material stiffness, or Young's modulus, in tendon is equivocal. Broad surveys of the Young's modulus of tendons in mammals and birds suggest that there is little variation between muscles or between species in the compliance of tendon as a tissue (Bennett et al., 1986; Bennett and Stafford, 1988; Pollock and Shadwick, 1994). However, there is evidence indicating tendon Young's modulus can vary with training effects (Buchanan and Marsh, 2001), between the aponeurosis and free tendon (Ettema and Huijing, 1989; Lieber et al., 1991), and even along the length of a single tendon (Lieber et al., 1991). Variation in Young's modulus in tendon is a particularly intriguing possibility as it may provide a mechanism for 'tuning' tendon properties to better coordinate integrated function with muscle contractile elements (Lieber et al., 1991).

The magnitude of fixed-end compliance suggest that for many muscles the ability to power movements depends upon the mechanical behavior of the tendon as much as it does the mechanical behavior of the muscle. A few studies have revealed some of the direct consequences of tendon length changes on the pattern of length change muscle contractile units undergo in vivo. Muscle length-tension curves can be shifted for a given joint position, and the operating range of the muscle–tendon unit is expanded by the action of series compliance (Lieber et al., 1992). Tendon length changes can uncouple muscle fiber length changes from joint movements, illustrated by the observation that during certain periods of the stride cycle in cats, gastrocnemius muscle fibers shorten while the muscle–tendon unit lengthens (Hoffer et al., 1989). It has been demonstrated that the very high power outputs at the ankle in jumping humans are possible only if fast rates of tendon recoil supplement the shortening of muscle contractile elements (Bobbert et al., 1986). The independence of joint movements and muscle fiber movements has important implications for the action of muscle spindle-mediated reflexes (Griffiths, 1991; Rack and Westbury, 1984), and it has been suggested that tendon compliance may act to simplify motor control for various types of movements (Rack and Ross, 1984). Tendon length changes can even affect muscle fascicle geometry during the course of a contraction; Narici et al. (1996) used ultrasonography on human gastrocnemius to show that fiber pennation angle and

physiological cross-sectional area varied over the course of an 'isometric' contraction as muscle fibers shortened against tendon compliance.

3. Tendon length changes during running

The utility of elastic energy storage and recovery during running results from the nature of the mechanical energy transformations that runners' bodies undergo. Each step a runner takes involves a cycle of energy (Cavagna et al., 1964). The limbs absorb kinetic and potential energy of the body as the center of mass falls and slows in the first half of the step. Mechanical work must be performed to reaccelerate and lift the center of mass in the second half of a step. Some of this cyclical work is done by contractile elements and some of it is done by the storage and recovery of strain energy in elastic elements. Muscle contractile elements use metabolic energy to perform work as well as to absorb it, but storage and recovery of elastic strain energy in tendons is independent of metabolic processes, and, at least at the level of the tendon, 'free'. The importance of elastic energy storage and recovery for running mechanics and energetics has been demonstrated with various experimental approaches. Analyses of mechanical energy changes of the body have shown that the cycle of kinetic and potential energy changes of the body are consistent with a spring-like function of the leg (Cavagna et al., 1977). The movements of the body and limb during running can be predicted by a model of a simple spring-mass system, (Blickhan, 1989; McMahon and Cheng, 1990), and different stride frequencies in large and small animals are reflected by differences in the resonant period of vibration of the leg-spring body-mass system (Farley et al., 1993). Energetic studies have demonstrated a lack of correlation between the mechanical work of running and the metabolic cost, supporting the idea that much of the cyclic mechanical work is performed by energy conserving mechanisms like elastic energy storage and recovery (Heglund et al., 1982). The energy-saving function of elastic elements in runners is often summarized with the intuitively appealing analogy of a bouncing ball; passive energy storage and recovery of mechanical energy provides some of the bouncing movement for free, reducing the work that muscles must do.

But why bounce? Unlike many other forms of locomotion, runners do little mechanical work to overcome external forces such as wind resistance, and the regular cycle of energy loss and recovery that the body undergoes with each step is not mechanically necessary to maintain forward motion at a steady speed. One might ask, do tendons reduce muscular work by powering the bounce of the body, or does the body bounce because muscles must transmit force through elastic tendons? Runners must support body weight cyclically, developing force with each footfall. Muscles require time to activate and deactivate, and therefore force does not rise and fall instantaneously with each footfall. The finite time of activation and deactivation of muscle contractile elements might explain the necessity of the bounce of the body during running; the body must accelerate downwards when vertical ground reaction forces are less than one body weight and accelerate upwards when forces are greater than one body weight. (The horizontal forces produced by a runner are also not necessary, on a strictly physical basis, to maintain constant-speed movement of the body, but they appear to be important for maintaining the alignment of the resultant ground reaction force and the limb; without them muscle forces would be very large due to a poor muscle mechanical advantage (Chang et al., 2000)). Thus, the elastic role of tendons during running may be necessary due to the limitations in muscle activation and deactivation times, and the necessary fluctuations in mechanical energy of the body that occur with a striding gait. This may explain in part why elastic compression and extension of the limb occurs even during walking, when total mechanical energy change of the body with each step is small (Lee and Farley, 1998). Interestingly, compared with large animals smaller animals' muscles activate more quickly (Close, 1972), and their tendons are proportionately stiffer (Pollock and Shadwick, 1994). The potential functional link between tendon stiffness and muscle activation/deactivation kinetics is unexplored.

Elastic mechanisms in runners save energy not just because they reduce the work muscles must do, but because they allow muscles to operate at shortening velocities that are favorable for economic force production (Taylor 1985; Taylor, 1994; Roberts et al., 1997). Independent of the mechanical energy fluctuations of the body, running animals moving at a steady speed must generate enough muscle force to support their body weight. Energetic studies have suggested that the

energy cost of generating this force can explain speed and size-related patterns of metabolic energy consumption during running (Taylor, 1985; Kram and Taylor, 1990). Muscles would consume metabolic energy to produce force during running even if they operated isometrically, allowing tendons to store and recover all of the mechanical energy fluctuations of the body. However, muscles should consume less energy to produce force if tendons do the work of running, due to two properties of skeletal muscle fibers. The first is the well known 'Fenn effect'; muscle fibers use more energy when they operate at higher shortening velocities and power outputs (Fenn, 1924). Thus, to the extent that the stretch and recoil of elastic tendons reduces the shortening velocity of muscle contractile elements, the energy consumed by each active fiber to produce force will be decreased. Second, and more importantly, the force–velocity relationship of skeletal muscle dictates that the force output of a skeletal muscle declines with increasing shortening velocity (Hill, 1938). A muscle fiber operating at intermediate shortening velocities to develop maximum power output produces one-third the force of the same muscle fiber contracting isometrically. Thus, the most significant advantage of the reduction in average shortening velocity and power output of muscles operating in series with energy-saving elastic elements is the effect that the force–velocity curve has on muscle recruitment. Fewer muscle fibers are active, consuming energy, if force is produced isometrically, than if the muscle operates at high shortening velocities and power outputs.

Direct measurements of muscle force, length and activity in running animals support the idea that the elastic function of tendon can allow muscles to operate at low shortening velocities, where force is produced economically. It has been demonstrated that the muscle fibers of the lateral gastrocnemius in running turkeys develop force but undergo little length change during stance phase of level running (Roberts et al., 1997). The direct effect of tendon compliance on the shortening pattern that the lateral gastrocnemius undergoes can be demonstrated by comparing estimated tendon length changes during stance with muscle fascicle length changes. Fig. 2 shows both length changes in the muscle fibers, measured by sonomicrometry, as well as the length changes that occur in the tendon, calculated from the measured tendon compliance (Fig. 1) and the muscle force.

If there were no tendon compliance, the muscle would have to undergo the lengthening–shortening pattern observed in the muscle–tendon unit to maintain the same joint movement. The stretch–shorten pattern of the tendon allows the muscle fibers to generate force nearly isometrically. The idea that this pattern of force development allows the muscle to develop force economically due to the effects of force–velocity properties on muscle recruitment is supported by observations of turkeys running uphill. The integrated EMG of the lateral gastrocnemius in running turkeys is three-fold greater during uphill running, when the muscle shortens and actively develops positive power, than when the muscle produces force nearly-isometrically during level running (Roberts et al., 1997). The increase in integrated EMG reflects the increased number of muscle fibers that must be active to provide force as muscle fibers operate at points on their force–velocity curves where higher powers but lower forces are developed.

The pattern of isometric force production due to tendon elastic energy cycling during steady-speed, level locomotion, has also been observed in hopping wallabies (Biewener et al., 1998) and walking humans (Fukunaga et al., 2001). Other studies of muscle length changes during running demonstrate that muscles also actively shorten and lengthen during steady-speed, level running (Carrier et al., 1998; Gillis and Biewener, 2001) and walking (Biewener and Corning, 2001). Future work may provide predictions for the factors that favor elastic recycling of energy during running vs. cyclic absorption and production of mechanical work in muscles.

4. Recruitment of tendons for different functions

The economy of tendon function results from the fact that its mechanical function is not coupled to metabolic processes. For activities like running, the passive storage and recovery of elastic strain energy can reduce muscular work and metabolic cost. The potential disadvantage of a passive structure such as tendons, in contrast to active muscle, is that tendon function cannot be independently turned on or off; tendons will always stretch and store energy as muscle force rises and will always recoil to release energy as muscle force declines. During an activity such as running, the energy stored in tendon can come from a decline in
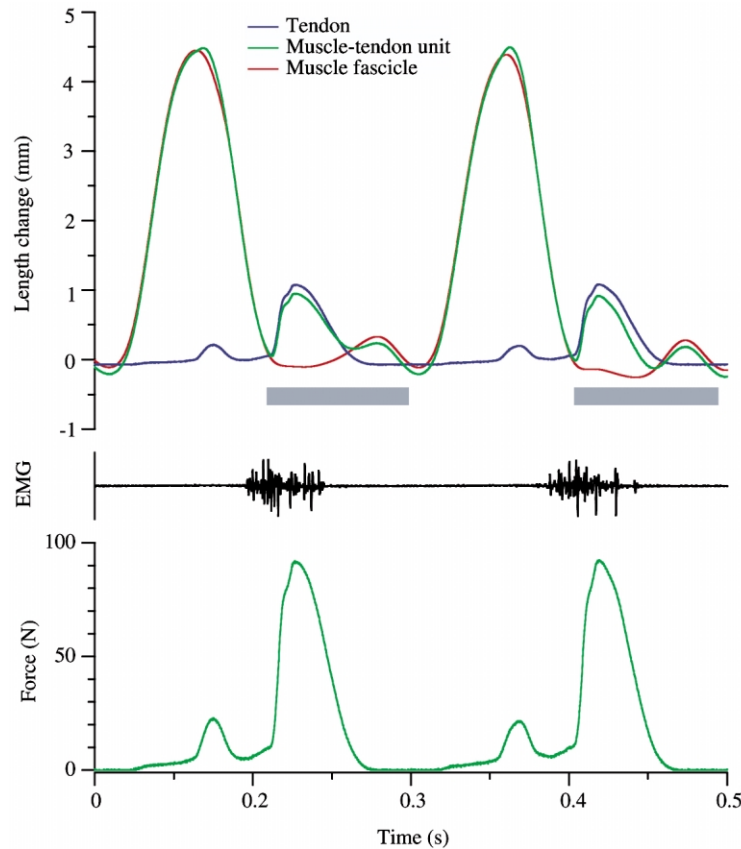
Fig. 2. Muscle fascicle, tendon, and muscle–tendon unit length change in turkey lateral gastrocnemius during representative running strides at 2.5 m s^{-1}. Muscle length change is arbitrarily referenced to the length at toe-down of the first stride. Length was measured by sonomicrometry and force was measured by strain gages glued to bony tendon (Roberts et al., 1997). Length changes of the tendon were estimated from the measured compliance of the tendon and the muscle force.

mechanical energy of the body. When the stored energy is recovered to lift and accelerate the body it reduces muscular work. For high power activities—those that require significant net mechanical work to increase the potential or kinetic energy of the body—the tendency of tendons to stretch can potentially increase the work muscles must do. If the energy stored during tendon stretch does not come from a decline in the energy of the body, as in running, it must come directly from work done by muscle fiber shortening. Because elastic elements can interfere with the direct transmission of muscle shortening to movements of the body, it has been suggested that muscles with shorter, stiffer tendons are best suited to provide power for movements such as jumping or accelerating (Alexander, 1974; Ker et al., 1988; Biewener and Roberts, 2000). Thus, architectural features of different muscles may particularly suit them to work vs.

force production, and specialization in muscle function could allow for activities like acceleration to be powered primarily by muscles with long fibers and little tendon compliance. Studies of a jumping dog support this idea (Alexander, 1974). The more proximal, less compliant extensors of the limb provide the power for jumping while the distal, compliant muscles operate as force-producing springs during both steady-speed running and jumping (Alexander, 1974).

It is well known, however, that for some high power activities the tendency of tendon elasticity to uncouple patterns of muscle shortening from patterns of body movements can enhance muscle performance. Elastic mechanisms in some jumping insects can act as muscle power amplifiers by directly storing the work done by muscle shortening and then releasing it rapidly (Bennet-Clark, 1975; Gronenberg, 1996). More recently, models
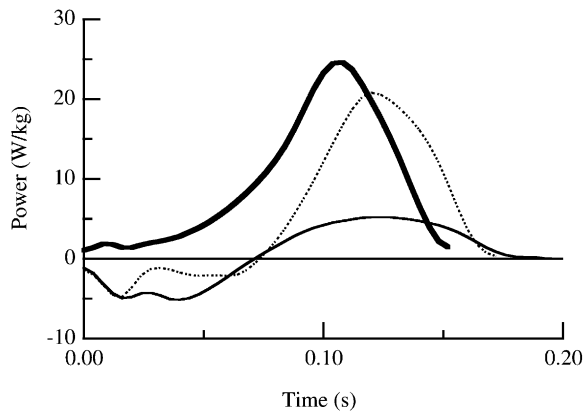
Fig. 3. Mechanical power output of the body during a single footfall in turkeys running at a steady speed (thin solid line), at a moderate acceleration (dotted line), and at a high acceleration (thick solid line). The asymmetric power profile is consistent with temporal redistribution of muscle work by elastic energy storage and recovery. Modified from Roberts and Scales (2002).

of human jumping have demonstrated that the series elastic component of ankle extensors can actually increase jump distance (Seyfarth et al., 2000; Bobbert, 2001). In modeled human jumpers, increasing the series elasticity increases muscle work output in a single jump because elastic mechanisms allow the muscle to operate at lower average shortening velocities and higher work outputs (Bobbert, 2001).

Studies of running accelerations in turkeys suggest that storage and recovery of muscle work by elastic mechanisms may play an important role in enhancing muscle power output not just in jumpers, but more generally for muscle-powered accelerations (Roberts and Scales, 2002). Two features of the dynamics of movement of the body during single footfalls in turkeys suggest that elastic mechanisms play an integral role during accelerations. First, the power turkeys develop during acceleration, measured by the rate of change of kinetic and potential energy of the body, is very low during the first half of a footfall and high during the second half (Fig. 3). This pattern is consistent with the idea that during the first part of stance, muscle work is stored directly as elastic strain energy as muscle contractile elements shorten against tendon stretch, and during the second half of stance this strain energy is released. Second, the peak instantaneous power developed late in stance during the highest accelerations exceeds

400 W kg^{-1} hindlimb muscle mass. This power output likely exceeds the power generating capacity of the hindlimb musculature, suggesting that some of the power contributed late in stance is released by elastic elements (Roberts and Scales, 2002).

Does elastic energy storage and recovery during inertial accelerations enhance muscle performance, or is it simply inescapable because many of the muscle–tendon units that contribute power to acceleration are relatively compliant? The ankle extensors and toe flexors in turkeys have short muscle fibers and long tendons, and they make up nearly half of the total extensor muscle mass. Thus, half of the potential muscle power output during an acceleration would be lost if compliant muscles–tendon units were specialized to act only as force-producing springs under all conditions. One explanation for the direct storage and recovery of muscle power by elastic elements is that it is unavoidable if all muscles are to be recruited to maximize mechanical power output during a burst activity like acceleration.

It is also possible that this power redistribution may be beneficial to performance; the temporal redistribution of muscle power output by storage and recovery in elastic elements may allow greater muscle power output and better performance during activities like acceleration. To examine the potential benefits of series elastic elements during an acceleration, I used a simple model of muscle-powered contraction, adapted from a model used to represent the elements of a muscle-powered acceleration in a frog jump (Roberts and Marsh, in preparation). The model consisted of a muscle operating across a lever to accelerate a mass. The model was constructed in the motion simulation program Working Model (Knowledge Revolution, Santa Ana, CA), using actuators with equations to simulate muscle contractile behavior and a linear spring to simulate tendon function. Muscle velocity was modeled on a Hill-type force–velocity equation, and activation and deactivation were a linear function of time. Maximum force, muscle length, and V_{max} were estimated to simulate the sum of turkey ankle extensors. Tendon fixed-end compliance was 20%. Upon activation, the muscle actuator produced force in proportion to velocity, length, and activation, and inertial and gravitational forces acted on the accelerated mass.

A muscle contraction during a steady-speed running step was simulated by giving the mass an
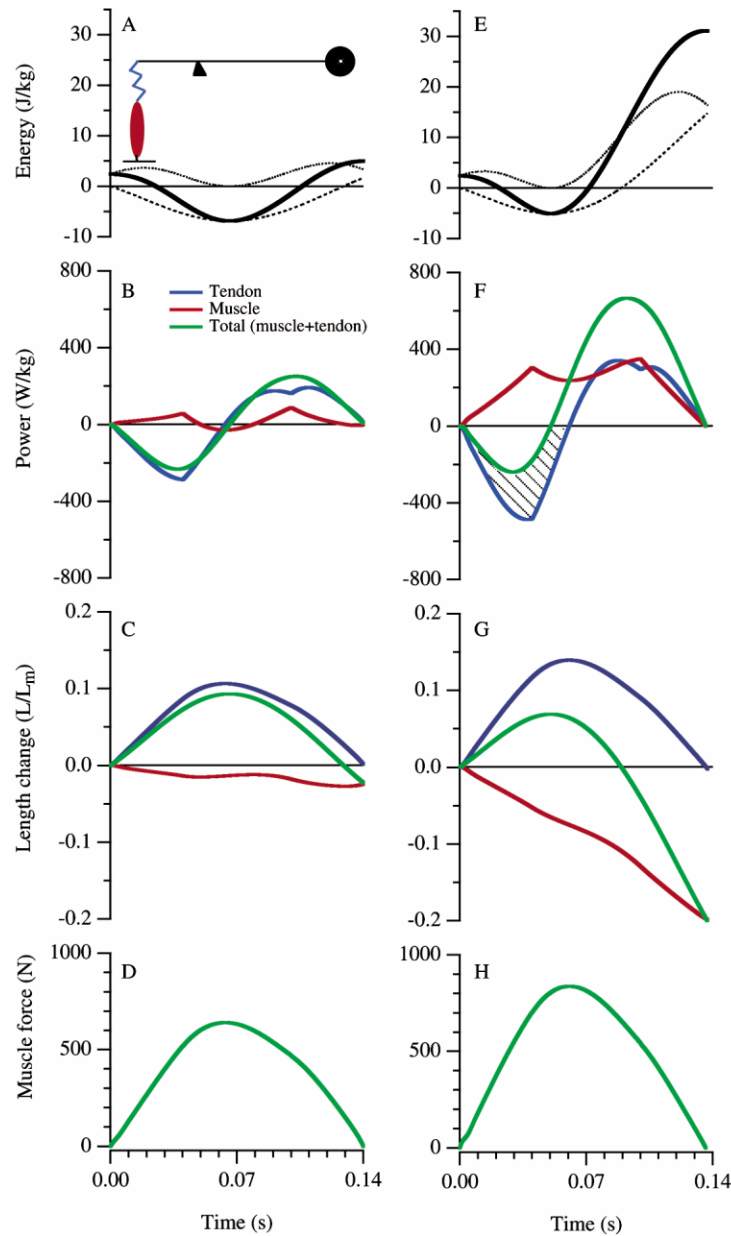
Fig. 4. Model output for a simulated muscle contraction during steady-speed running (left hand column) and acceleration (right hand column). Dynamics of the muscle contractile element (red), tendon (blue), combined muscle–tendon unit (green) and the body (black) were monitored for a single simulated contraction. Energy values are presented for kinetic (dotted line), potential (dashed line) and total energy (solid line). During the steady-speed simulation, energy changes of the body were stored and recovered in the tendon and little muscle power was developed. During the acceleration simulation muscle power output was relatively constant and high when the muscle was fully active. Muscle work was stored as elastic strain energy (hatched area) and released later in the stride. Peak tetanic force of the muscle (P_o) was set to 600 N for the steady-speed simulation, and 1200 N for the acceleration. All other parameters were the same for both simulations. Power and energy values are expressed per kg muscle mass.

initial downward velocity of 0.3 m s^{-1} at the onset of muscle activation. Once the simulation began, the movement of the muscle, tendon and mass were determined only by muscle–tendon proper-

ties and inertial and gravitational forces on the mass. Steady-speed running involves submaximal recruitment of muscle fibers (Armstrong et al., 1977). Maximal muscle force was 600 N, half of

estimated maximal force for the ankle extensors, to simulate recruitment of half of the muscle fibers during steady-speed running. The left column of Fig. 4 shows that under these conditions, the mechanical behavior of the muscle, tendon, and body mass were similar to that expected during steady speed, level running. The energy of the body declined as the body slowed and lowered, and then increased as the body reaccelerated and rose to slightly higher than its initial position (Fig. 4A). Most of the energy change of the body was stored and recovered in the tendon, and the power profile of the tendon closely matched that of the body (Fig. 4B). The muscle produced force, but underwent little length change and therefore developed little mechanical power (Fig. 4C, D).

To determine whether the modeled system could both minimize muscular work in a contraction that simulates steady speed running and effectively deliver muscle power for an acceleration, the maximum force output of the muscle was doubled. This simulated maximal muscle recruitment that might be expected during a maximal acceleration. All other muscle/tendon parameters and initial conditions were identical in the two simulations. The results for the simulated acceleration are presented in Fig. 4 (right hand column). The pattern of force development and the pattern of energy storage (negative power) and recovery (positive power) by the tendon were similar in both steady-speed and acceleration simulations. The time of the contraction was also similar. The most striking difference between the two contractions was in the length change and power output of the muscle. The muscle shortened during the entire contraction, and developed relatively high power outputs throughout, despite the fluctuations in mechanical power applied to the body (Fig. 4F, G). As in the steady-speed simulation, the tendon stored energy in the first half of the contraction and released it in the second half of the contraction. The difference was in the source of this stored energy. Some of the elastic strain energy stored resulted from a decline in the energy of the body, but more than half the energy stored in tendon came directly from contraction of muscle contractile elements (Fig. 4F, G). The shaded area in Fig. 4F represents the work done on tendon directly by muscle shortening. Muscle power output was relatively constant when the muscle was fully active.

These simulations are based on a model of muscle-powered acceleration that is greatly sim-

plified from the complex interactions that occur between muscles and across joints during natural limb movements, but the results illustrate relevant principles about interaction of muscles, tendons, and inertial loads during locomotion. First, these simulated contractions illustrate how energy loaded into a tendon directly by muscle shortening can be recovered to help accelerate a body. The mechanical energy produced by muscle shortening against tendon compliance is not lost but is recovered to power movements of the body at a later time. There is also no necessary delay in time associated with the accelerative contraction; both contractions are of approximately the same duration. The high, steady muscle power output observed during the simulated acceleration demonstrates a potential advantage of storage and recovery of muscle work in tendons during accelerations. Despite the fluctuation in power applied to the body, the power output of the muscle is relatively constant, initially working against tendon compliance and later working to directly power movement of the body. Without a tendon, the power output of the contractile element during the first part of the contraction would be necessarily negative and/or low until the downward velocity of the body had been reversed and increased. Finally, the muscle–tendon interaction observed in this contraction may actually illustrate a simple strategy for motor control. The dramatic difference in muscle shortening and power applied to the body in the two simulations was achieved by simply increasing muscle recruitment (simulated by increasing maximum force). Recruiting a greater number of muscle fibers caused the muscle to shorten against the tendon, and as a result the function of the tendon changed, from primarily storing and recovering energy changes of the body (during steady-speed running) to storing and recovering muscle work (during simulated accelerations). Interestingly, the doubling of recruitment by doubling maximal muscle force resulted in an increase in muscle force during the simulated contraction of only 30% (Fig. 4D, H). The increase in peak tetanic force caused the muscle to operate at higher shortening velocities and over a region of the force–velocity curve where relatively lower forces were developed. A simple change in muscle recruitment changed the pattern of shortening of the muscle fibers and the function of the tendons, to produce a very different pattern of movement of the body over a single contraction. As a result of the change in muscle

recruitment, tendon is recruited to store and recover muscular work.

The redistribution of muscle work in time by elastic energy storage and recovery during acceleration may represent a more general example of the specialized case of elastic energy storage and recovery in specialized jumpers. It has been recognized that the ability of elastic structures to act as muscle power amplifiers is important in jumping, where a single muscle contraction must be performed in a limited amount of time to increase the energy of the body (Bennet-Clark, 1975; Alexander, 1995). The most spectacular examples of elastic jumpers are insects such as fleas and locusts that use a catch mechanism to allow muscle contraction before the jump to store energy in elastic structures, then release the catch to allow the rapid recovery of elastic energy in a brief burst of mechanical power to accelerate the body (reviewed by Gronenberg, 1996). Some vertebrate jumpers also appear to use elastic mechanisms to enhance power output during a jump. Galagos and some species of frogs produce power outputs during a jump in excess of available muscle power (Aerts, 1997; Marsh, 1999). The power profiles of the body in these jumpers are similar to those observed in our model above, and similar to the power profile observed for accelerating turkeys. Taken together, these observations suggest that energy may be stored early in the jump in elastic structures and released later in the jump. Elastic energy storage and recovery may also be important in non-specialized jumpers, including humans (Bobbert et al., 1986; Seyfarth et al., 2000; Bobbert, 2001). The observation that it plays a significant role during acceleration suggests that elastic energy storage and recovery may be generally important in muscle-powered movements that accelerate inertial loads.

5. Conclusions

The pattern of length change and power output of muscle contractile elements is determined, to some degree, by the length changes that elastic tendons undergo during muscle contraction. Our increasing understanding of muscle function in vivo is revealing that the tightly integrated and complementary function of elastic elements and muscle contractile elements may be necessary for muscle force and power development over favorable regions of the force–velocity curve, under favorable patterns of activation/deactivation, and at favorable lengths. In the future, more general principles of the mechanical function of muscle–tendon units as integrated actuators will provide greater predictive power and more compelling explanations for the locomotor modes, systems, and muscles that utilize compliant tendons to enhance muscle function.

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