

Understanding Muscle Energetics in Locomotion: New Modeling and Experimental Approaches

Brian R. Umberger¹ and Jonas Rubenson²

¹Department of Kinesiology, University of Massachusetts Amherst, Amherst, MA; and ²School of Sport Science, Exercise and Health, The University of Western Australia, Crawley, Western Australia, Australia

UMBERGER, B.R. and J. RUBENSON. Understanding muscle energetics in locomotion: new modeling and experimental approaches. *Exerc. Sport Sci. Rev.*, Vol. 39, No. 2, pp. 59–67, 2011. *Recent estimates of muscle energy consumption during locomotion, based on computational models and muscle blood flow measurements, demonstrate complex patterns of energy use across the gait cycle, which are further complicated when task demands change. A deeper understanding of muscle energetics in locomotion will benefit from efforts to more tightly integrate muscle-specific approaches with organismal measurements.* **Key Words:** walking, running, skeletal muscle, musculoskeletal modeling, blood flow, oxygen consumption

INTRODUCTION

Improving our knowledge of how muscles use metabolic energy to perform specific mechanical tasks during walking and running is central to our basic understanding of terrestrial locomotion. Such enhanced knowledge would inform theories on how organismal energy consumption scales with size and varies with body design (bipedal and quadrupedal) and gait form (walking and running) (21,28). A richer comprehension of the energetic function of muscle during locomotion also has important clinical implications, as many gait disorders are characterized by an elevated cost of locomotion (35). The ability to routinely quantify organismal oxygen consumption (a proxy for metabolic energy consumption) is fundamental to our current understanding of locomotor energetics. Further insight could be gained from knowledge of the energy use by individual muscles during locomotion. Unfortunately, direct measurement of individual muscle oxygen consumption in all of the active muscles during dynamic activities is not technically feasible (13). Thus, inferences regarding muscle energy demand and its association with different gait functions have typically relied on organismal measurements. A common approach has been to evaluate differences in organismal energy

expenditure across different movement speeds, inclines, body sizes, or loading conditions. Although the changes in organismal energy consumption across conditions do reflect changes in total muscle energy demand, specific links between muscle energy use and locomotor mechanics are harder to establish.

Recently, two new approaches have begun to shed additional light on muscle energetics in locomotion. One of these is a computational approach (Fig. 1) and involves generating computer simulations of locomotion (17,36), in conjunction with a model for predicting energy consumption in individual muscles (e.g., (1,10,33)). This approach is computationally demanding but provides estimates of metabolic energy consumption for each modeled muscle. The other technique is experimental in nature (Fig. 1) and involves measuring muscle blood flow, which has been shown to be directly proportional to muscle oxygen consumption for aerobic conditions (13). This approach is technically challenging but provides estimates of the distribution of energy use across individual muscles or muscle groups. Recent studies based on these two techniques have provided important new perspectives on the energetics of muscle in locomotion. Results from these studies have sometimes supported, and other times challenged, conclusions from earlier studies based on organismal energy consumption. Many avenues are available to advance our understating of locomotor energetics. Organismal energy consumption has frequently been combined with anatomical data, biomechanical analyses, and external devices for isolating some aspect of locomotion (e.g., (3,7,20,25,30,32)). Here, we focus on recent efforts where organismal measurements were combined with estimates of energy use in individual muscles. We present an integrated view of our own research based on computational modeling (Umberger) and muscle blood flow techniques (Rubenson),

Address for correspondence: Brian R. Umberger, Ph.D., Department of Kinesiology, University of Massachusetts Amherst, Amherst, MA 01003-9258
(E-mail: umberger@kin.umass.edu).

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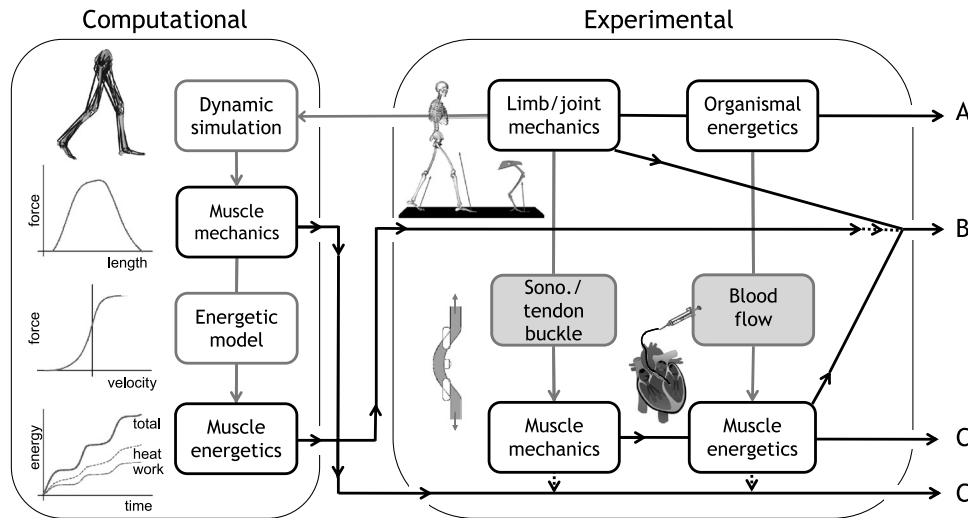


Figure 1. Flow chart summarizing computational and experimental approaches for evaluating the energetics of locomotion. There are three exit points from the flow chart reflecting the availability of different combinations of experimental and/or simulation data. Exit point A represents cases where the available data are insufficient to draw strong conclusions regarding the detailed energetic function of muscle. Exit point B represents cases where inference can be drawn regarding the energetic function of muscle with respect to specific gait tasks, such as swinging the limb or supporting body mass. Exit point C represents cases where inference can be drawn regarding the energetic function of muscle with respect to the mechanical roles of individual muscles, such as the efficiency of performing mechanical work. Sono., sonomicrometry.

in the context of other closely related literature. Our premise is that combining organismal measurements with muscle-specific energy estimates is an especially promising approach for accelerating our understanding of locomotor energetics.

ESTIMATING INDIVIDUAL MUSCLE ENERGY CONSUMPTION *IN VIVO*

The two primary techniques used in the studies discussed in this review differ greatly, yet they have the same ultimate goal: to provide estimates of the metabolic energy consumed by individual muscles during unrestrained locomotion. The computational approach is based on modeling, simulation, and optimization techniques, which have become common tools for studying the mechanics, energetics, and control of locomotion (17,36). At the heart of any musculoskeletal model is a mechanical muscle model, which characterizes the static and dynamic response characteristics of muscle to excitation by the nervous system. A model for predicting muscle energy consumption was developed by Umberger *et al.* (33) as an extension to the underlying mechanical muscle model. This model predicts the rate of heat production (\dot{h}) and the rate at which mechanical work is done (\dot{w}), based on the activation and contractile state of the muscle. Other muscle energetics models have generally been formulated in a similar manner (*e.g.*, (1,10)). A typical expression for the rate of muscle metabolic energy consumption (\dot{E}) is

$$\dot{E} = \dot{h}_A + \dot{h}_M + \dot{h}_{SL} + \dot{w} \quad (1)$$

where \dot{h}_A is the activation heat rate, associated with non-contractile costs (*e.g.*, operating ion pumps); \dot{h}_M is the maintenance heat rate, directly associated with cross-bridge cycling; \dot{h}_{SL} is the additional rate of heat production during fiber shortening or lengthening; and \dot{w} is the mechanical power of the contractile part of the muscle model. From basic

thermodynamic consideration, the sum of the heat and mechanical work is equal to the total metabolic energy consumed. By summing metabolic energy consumption over all of the muscles in the model, one arrives at a value that corresponds closely to the net (exercising minus resting) energy consumption that is measured in experimental subjects.

The experimental approach for estimating energy use in individual muscles is based on the premise that, under aerobic conditions, the blood flow rate to an active muscle is proportional to its metabolic rate (13). Excellent agreement between increases in total blood flow rate to leg muscles and organismal metabolic rate has been observed in walking and running guinea fowl *Numida meleagris*, an approximately 1.5-kg bird (Fig. 2) (13,22), and between regional muscle blood flow rates and muscle metabolic rates in aerobically exercising humans (reviewed in (13)). The distribution of energy expenditure among active muscles during locomotion can thus be determined by measuring the proportion of the total blood flow rate attributed to each muscle. Combining these data with organismal energy expenditure allows estimates of muscle-specific metabolic rates (24).

A series of recent studies on guinea fowl have adopted an injectable microsphere technique, pioneered by R. L. Marsh, to assess individual muscle blood flows during locomotion (5,14,22). Polystyrene microspheres containing colored dyes are injected into the circulation via the left ventricle and become trapped in the systemic capillaries. The number of microspheres in each of the muscle tissues is determined *post mortem*. By combining the number of microspheres in a reference arterial blood withdrawal of a known flow rate, one can calculate the specific tissue blood flow rate (\dot{Q}_t , mL·min⁻¹) as

$$\dot{Q}_t = \frac{\dot{Q}_b N_t}{N_b} \quad (2)$$

where \dot{Q}_b is the reference blood withdrawal rate (performed simultaneously with the microsphere injection) and N_t and

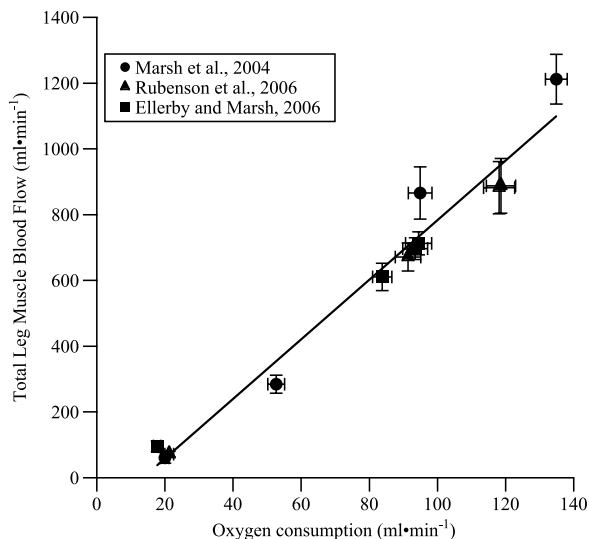


Figure 2. Relation between mean blood flow to the leg muscles and mean organismal oxygen consumption for a range of walking and running speeds in guinea fowl. The line is a regression line through all of the data (slope = 9.1 ± 1.2 , 95% confidence interval). Values are means \pm SEM ($n = 5-8$). Circles: Marsh *et al.* (14); triangles: Rubenson *et al.* (22); squares: Ellerby and Marsh (5). [Adapted from Marsh RL, Ellerby DJ. Partitioning locomotor energy use among and within muscles: Muscle blood flow as a measure of muscle oxygen consumption. *J. Exp. Biol.* 209:2385-94. Copyright © 2006 The Company of Biologists Ltd. Used with permission.]

N_b are the number of microspheres in the tissue sample and blood withdrawal, respectively. To assess the effect of different experimental conditions on regional muscle blood flow rates (e.g., speed, incline, loading), a series of injections using different colored dyes for each condition is used, typically including a baseline resting measurement.

MUSCLE ENERGY USE OVER THE GAIT CYCLE

The relative costs of the various phases of the gait cycle have been the topic of considerable debate in the literature. Recently, there has been a particular interest in the long-standing question of how much metabolic energy it costs to swing the leg in walking and running. The nineteenth-century scientists Wilhelm and Eduard Weber likened the swinging limb to a passive pendulum, implying a limited muscular cost. Further evidence that the cost of swinging the leg is low came from comparative studies by Taylor and colleagues (29) where locomotor costs were found to increase in direct proportion to loads added near the center of mass of the body and were independent of limb mass and moment of inertia in animals of similar total body mass (30). In both cases, the trends that were found in organismal energy consumption would not be expected if swinging the leg represented a substantial proportion of the total cost of locomotion. The conclusion that leg swing costs are negligible factored heavily into the development of a prevalent theory of locomotor costs (27). According to the force hypothesis, the metabolic cost of locomotion is determined primarily by the cost of generating muscular force when the foot is in contact with the ground (27). However, there is other evidence that suggests leg swing may be costly. For example, a recent study of isolated leg swinging in humans

indicated that leg swing may represent as much as one third of the net cost of walking (3). A contemporary extension to the original force hypothesis also explicitly includes forces associated with leg swing in the prediction of locomotor costs (18).

Deeper insight into the debate over the cost of leg swing in locomotion would be possible if the metabolic energy consumed by muscles (if any) during the swing phase could be determined. Ellerby and Marsh (5), Marsh and coworkers (14), and Rubenson and colleagues (22) used muscle blood flow measurements to obtain the first estimates of relative swing phase energy consumption in recent studies of walking and running in guinea fowl. In the particular species of bird studied, nearly all locomotor muscles are active during only the swing phase or only the stance phase, making it possible to partition the total cost of locomotion between these two phases (14). In one large thigh muscle (femerotibialis), whose activity spans the stance and swing phases, blood flow was divided evenly between the two phases, although Rubenson and Marsh (24) noted that the results were relatively insensitive to this assumption. The major findings of these studies were that muscles active during the swing phase accounted for approximately 25% of the total leg muscle blood flow (Fig. 3A), indicating that the metabolic cost of swinging the leg is not trivial.

Although guinea fowl exhibit a number of interesting locomotor similarities with humans, there are obvious differences, and one might wonder whether these results generalize to humans. Recent experimental studies on the cost of leg swing in human walking have yielded intriguing, albeit inconsistent, results. One study, in which leg swing was assisted passively by an elastic device, indicated that swinging the leg represented 10% of the net cost of walking (7), whereas the aforementioned study on isolated leg swinging yielded an estimate of 33% of the net cost (3). These studies, based on organismal energy consumption, were among the first to identify the independent cost of limb swing in human locomotion. Nevertheless, even with these tightly controlled experimental designs, it is difficult to completely isolate (7) or replicate (3) the mechanics of leg swing in walking using experimental procedures in humans.

Recently, Umberger (31) addressed the question of leg swing costs in human walking using a musculoskeletal modeling approach. A forward dynamics simulation of walking at a comfortable speed ($1.3 \text{ m}\cdot\text{s}^{-1}$) was generated, and the metabolic energy consumed by each muscle in the model was predicted using the muscle energetics model described earlier (33). Unlike guinea fowl, in humans, several muscles are active in both the swing and stance phases. However, because the instantaneous rate of muscle energy expenditure in the model was known over the full gait cycle, it was possible to partition energy use into the swing and stance phases. The major finding was that swing phase energy consumption represented 29% of the total muscular cost (Fig. 3B), which was similar to the percentage ($\sim 25\%$) reported for guinea fowl (14,24). The consistency of results in two different species using very different methods indicates strongly that leg swing in locomotion accounts for approximately 25%–30% of the cost of locomotion, with the remaining 70%–75% being associated with stance phase muscle actions. Although the greatest amount of energy is consumed by muscles during the stance phase,

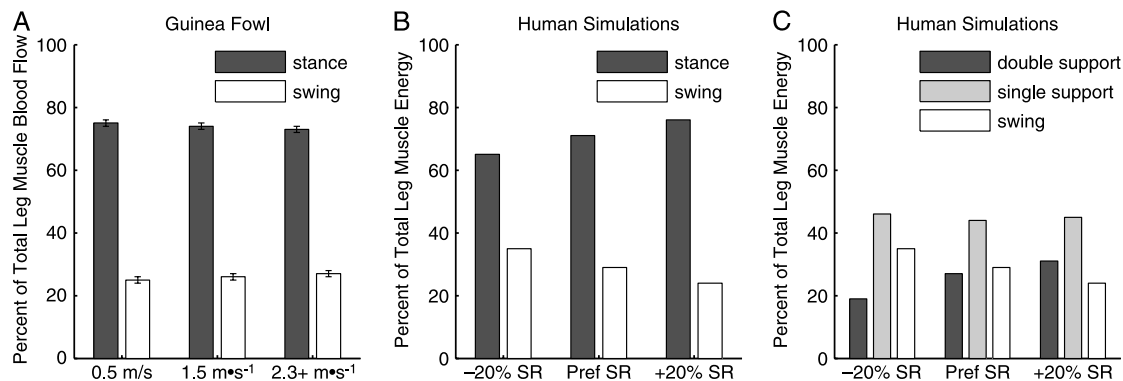


Figure 3. Partitioning of stance and swing phase locomotor costs. A. Percentage of total hind limb muscle blood flow to the combined stance and swing phase muscles for walking ($0.5 \text{ m}\cdot\text{s}^{-1}$) and running (1.5 and $2.3+ \text{ m}\cdot\text{s}^{-1}$) in guinea fowl. The highest aerobic running speed ranged from 2.3 to $2.8 \text{ m}\cdot\text{s}^{-1}$ across birds (based on data from Marsh *et al.* (14) and Rubenson *et al.* (22)). B. Percentage of total leg muscle energy consumption during the stance and swing phases in computer simulations of human walking ($1.3 \text{ m}\cdot\text{s}^{-1}$) at the preferred stride rate (Pref SR), as well as stride rates 20% lower (-20% SR) and higher ($+20\%$ SR) than preferred (based on data from Umberger (31)). C. Same data as in panel B but with stance phase energy consumption partitioned into double-limb and single-limb support periods.

any theory that seeks to explain the energetics of locomotion in a general sense will need to account for the costs incurred by muscles during the swing phase.

The recent muscle blood flow and modeling studies also have illuminated how and when muscles consume energy during the stance phase. Kuo *et al.* (9) suggested that most (60%–70%) of the net energy consumption in bipedal walking is required to affect the transitions from step to step, roughly corresponding with the double-limb support periods, when both feet are on the ground. However, Neptune *et al.* (17) argued that single-limb support cost may be substantial, as muscles must generate force and perform work to stabilize the leg and raise the center of mass during single-limb support. Based on the same simulations of human walking used to estimate leg swing costs, Umberger (31) found the single-limb support period to represent 44% of the total muscle energy consumption, whereas the two double-limb support periods combined accounted for 27% (Fig. 3C). However, step-to-step transitions may actually extend beyond the double-limb support period (9); thus, 27% may underestimate transition costs. When a longer transition interval was accounted for, the predicted step-to-step transition cost was higher, at 37% of the total muscular cost (31). If some of the positive work required to drive the step-to-step transitions occurs elsewhere in the gait cycle (9), then this may indeed be the task that consumes the greatest amount of metabolic energy in walking but perhaps by a considerably lesser amount than previously suggested. The analyses summarized here provide prime examples of using estimates of muscle energy consumption to gain insight as to the energetic function of muscle with respect to specific gait tasks (exit point B in Fig. 1).

An advantage of having estimates of metabolic energy use in individual muscles is that it is possible to probe beyond the simple cost accounting of various gait cycle intervals, such as understating why energy consumption during double-limb support was predicted to be relatively low. The rate of muscle metabolic energy expenditure in the simulation model was actually highest during the first double-limb support period (*i.e.*, in the leading limb), with the hip extensor and knee extensor muscles consuming the most energy (Fig. 4). Double-limb support as a whole did not represent a greater percentage

of the total cost of walking not only because these intervals are relatively brief but also because the rate of muscle energy consumption was lowest during the second double-limb support period (*i.e.*, in the trailing limb) (Fig. 4). Energy consumption in the trailing limb was low during double-limb support, as the plantar flexors were the only muscle group consuming energy to any substantial degree.

Estimates of energy use in individual muscles also provide information on how energy consumption in locomotion is distributed across the muscles associated with each of the major lower limb joints. Here, we provide a direct comparison based on the human simulation results reported by Umberger (31)

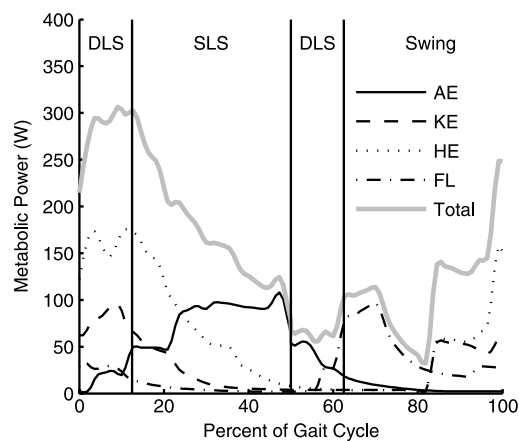


Figure 4. Instantaneous metabolic power for all of the muscles in a single limb across the gait cycle in a computer simulation of human walking ($1.3 \text{ m}\cdot\text{s}^{-1}$) at the preferred stride rate (54 stride/min). Heel strike of the ipsilateral limb corresponds to 0 and 100% of the gait cycle. The stride is partitioned into double-limb support (DLS) and single-limb support (SLS) periods and the swing phase. HE (hip extensors) is the sum of glutei, medial hamstrings, and biceps femoris longus; KE (knee extensors) is the sum of vasti and rectus femoris; AE (ankle extensors) is the sum of gastrocnemius, soleus, and "other" plantar flexors; FL (flexors) is the sum of iliopsoas, biceps femoris brevis, and dorsiflexors; and Total is the sum of all muscles. [Adapted from Umberger BR. Stance and swing phase costs in human walking. *J. R. Soc. Interface.* 2010; 7:1329–40. Copyright © 2010 The Royal Society. Used with permission.]

and the muscle blood flow measurements in guinea fowl from Rubenson *et al.* (22). For this analysis, muscles were grouped according to the joint at which they exert their primary influence during gait; for example, the gastrocnemius was grouped with the ankle extensors, despite its flexion moment arm at the knee (see (22) and (31) for more detail). Interestingly, the distribution of energy consumption (Fig. 5) was found to be similar across the hip, knee, and ankle in the human walking simulations and the guinea fowl experiments (4,22,31), mirroring the similar stance/swing phase costs in humans and birds. Hip extensor muscles consumed the greatest percentage of the total muscle energy expenditure (human model, 40%; guinea fowl, 40%). In contrast, knee extensor muscles consumed considerably less energy (human model, 18%; guinea fowl, 13%). The relatively low costs incurred by knee extensor muscles occurred in the face of considerable cocontraction of knee extensor and flexor muscles, which seems to be crucial for stabilizing the knee joint (4,17). In the absence of the need to stabilize the knee, the costs incurred by the knee extensors presumably could be even lower, approximating the ideal of the inverted pendulum model. The results for the ankle extensor muscles (plantar flexors in humans and combined ankle extensors and digital flexors in birds) were intermediate to the hip and knee (human model, 27%; guinea fowl, 29%). The remainder of the metabolic energy was consumed by muscles that primarily flex the joints, largely during the swing phase (human model, 15%; guinea fowl, 18%). The distribution of energy consumption summarized here is in qualitative, if not quantitative, agreement with the study by Sawicki *et al.* (25) in humans, based on joint work and organismal energy consumption. A common theme is that the hip muscles are the primary energy consumers, with the ankle plantar flexors consuming less energy, despite generating considerable mechanical work. The plantar flexors seem to achieve this high overall mechanical efficiency by exploiting storage and release of tendon elastic energy (17,25) and by performing work partly during deactivation (31), which is an especially economical mode of operation (12).

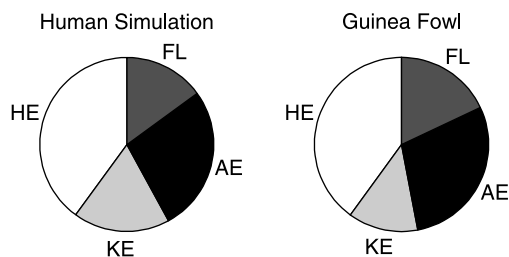


Figure 5. Distribution of muscle energy consumption across the major joints of the lower limb. *Left panel:* distribution of muscle energy consumption across muscle groups for a computer simulation of human walking ($1.3 \text{ m}\cdot\text{s}^{-1}$) (based on Umberger (31)). *Right panel:* distribution of total hind limb muscle blood flow across the muscle groups for running ($1.5 \text{ m}\cdot\text{s}^{-1}$) in the guinea fowl (based on Rubenson *et al.* (22)). HE (hip extensors), KE (knee extensors), AE (ankle extensors: plantar flexors in humans, combined ankle extensors and digital flexors in birds), and FL (flexors combined across all joints). Although the speeds compared for humans and guinea fowl were similar, the human data were for walking, whereas the birds were running. However, the energy distribution across joints for guinea fowl is quite stable across walking and running speeds on level ground, particularly for the HE and AE muscles (4).

MUSCLE ENERGY USE WITH CHANGING TASK DEMANDS

When only organismal energy expenditure is available, investigators are forced to make assumptions regarding the distribution of energy use among muscles that occurs with changing task demands. This makes generating conclusions on the energetic function of individual muscles difficult. For example, it often is assumed that trunk and limb loading only increase metabolic energy use in stance and swing phase muscles, respectively (*e.g.*, (29)). Augmenting organismal energy consumption with measurements of muscle blood flow in individual muscles in guinea fowl has illuminated a number of these issues. Ellerby and Marsh (5) found that energy use in swing phase muscles increased significantly as a result of trunk loading, clearly affecting interpretations of the muscular cost of supporting body weight and accelerating mass during stance. Furthermore, limb loading increases the energy use of stance phase muscles markedly (5), which may reflect the cost of accelerating the loaded segment during stance (15) or the cost to initiate limb swing. Energy use in an individual muscle may even decrease, in conjunction with an increase in organismal energy consumption, such as in the gastrocnemius intermedia during trunk loading (5). Together, these results demonstrate the benefit of having estimates of energy use in individual muscles to complement organismal energy data.

More generally, estimates of muscle energy consumption across different locomotor conditions have helped establish important links between the mechanical roles of muscles during different locomotor task and their associated energy cost. Studies involving manipulations of speed, cycle frequency, loading, and incline illustrate this particularly well. For example, the relative costs of muscle actions during the stance and swing phases in guinea fowl were reported to be stable across the full range of aerobically supported walking and running speeds (Fig. 3A) (14). This is surprising perhaps, as the distribution of blood flow to individual stance and swing phase muscles varied considerably with speed, yet the blood flow summed across muscles always was approximately 75% of the total for stance phase and 25% for swing phase. However, other locomotor conditions have shown stance and swing phase costs to be mutable. The relative stance/swing phase costs in human walking simulations were found to vary when stride frequency and stride length were changed, with speed held constant (31). The relative cost of leg swing was reported to increase for walking with long, slow strides, whereas it decreased for walking with short, quick strides (Fig. 3B). Loading and incline studies also have demonstrated changes in stance and swing phase costs. Running with trunk loading (5) or running uphill (22) leads to disproportionately higher stance phase costs, whereas running with distal limb loading (5) increases relative swing phase costs.

Locomotion studies where task demands were altered also have provided information on muscle energetics that go beyond the relative stance/swing phase costs. Interestingly, Ellerby *et al.* (4) found that less than a third of the muscle mass recruited during running in guinea fowl shows increases in energy cost that parallel the increase in organismal energy expenditure across a full range of speeds. The remaining muscles either increase their energy use primarily between rest and slow

speeds (such as fibularis longus, an ankle extensor) or between moderate and faster speeds (such as the gastrocnemius muscles). The reason for this may be explained by fiber type distributions; muscles with primarily slow fibers are preferentially recruited at slow speeds, and those with mostly fast fibers are preferentially recruited at faster speeds, whereas muscles with a mixed fiber distribution are recruited evenly across all speeds (4). A complementary effect of fiber type distribution on locomotor energetics was described by Umberger *et al.* (34), based on computer simulations of human pedaling. Varying the percentage of slow and fast muscle fibers in a musculoskeletal model, within the range typically observed in humans, led to changes in total metabolic cost (~25% higher in the model with more fast fibers) and in the pedaling cadence predicted to maximize muscular efficiency (12 rpm higher in the model with more fast fibers). Taken together, these experimental and modeling results imply that muscle fiber type distribution is an important determinant of both the specific muscles recruited to meet the demands of a movement task and the movement pattern that is optimal from an energetic perspective.

Regional blood flow experiments during trunk loading also have revealed more specifically how muscle activation patterns may function to minimize energy use. The additional energy consumed because of the added weight to the back of the guinea fowl occurs nearly exclusively in either one- or two-joint hip and knee extensor muscles (5). Little increase in energy use occurs in two-joint muscles that flex the knee. The conclusions from this study were that this uneven distribution of energy use represents a strategy whereby additional body support and propulsion is achieved in the absence of antagonist joint moments, that would otherwise result in a higher energy cost because of cocontraction (5).

Finally, the experiments on incline running by Rubenson *et al.* (22) have reinforced proposed links between muscle architecture and energetic function. Running uphill results in elevated metabolic energy expenditure, owing to the additional mechanical work done against gravity. Blood flow data on guinea fowl running uphill demonstrate the following: the increase in energy use occurs primarily in long, parallel fibered muscles with little external tendon, consistent with the theory that muscle-tendon architecture modulates mechanical work production (2); pinnate fibered muscle also contributes significantly to increases in energy use, indicating that they likely also are important in generating mechanical work; and most of the increase in energy use occurs in muscles whose primary action is at the hip, corroborating the finding that the hip plays a major role in generating the additional work of incline running (19). Here, the integration of muscle-specific metabolic data with organismal measurements helped verify proposed links between muscle-tendon architecture and locomotor function in uphill running (2,6), while allowing more direct connections to be made with muscle energy use *per se* (22).

LINKING MUSCLE FORCE, WORK, AND METABOLIC COST

Researchers have long sought to link muscle force and work with the energetics of terrestrial locomotion. The laws of mechanics and thermodynamics provide the necessary

framework, yet our understanding of how multiple muscles function together during locomotion remains incomplete. Measurements of organismal energy consumption have been paired with biomechanical analyses by both present authors (20,23,32) and several other research groups (*e.g.*, (3,7,9,29)), providing important information on general links between locomotor mechanics and energetics. However, these techniques lack the resolution necessary to establish these relations at the muscular level. In addition to the challenges associated with quantifying muscle energy use, the other major impediments to progress on this front are the difficulties in measuring muscle force and work in individual muscles during locomotion. There are some limited situations where a computed joint moment or power can be related uniquely to muscle force or power, as when a single muscle is known to be the only major contributor to a net joint moment (*e.g.*, (24)). However, whole-body, segment, or joint measurements usually do not provide information on the mechanics of individual muscles because of the redundancy of the musculoskeletal system. Computational models and direct measurements both provide a means for bridging this gap.

Musculoskeletal models can be used to generate simulations that replicate locomotor movements, yielding force and displacement histories for each modeled muscle. Modeling studies have advanced our understanding of the mechanical energetics of locomotion (17,36), yet they usually reveal little about the metabolic cost of the associated muscle actions (17). Several investigators have used muscle energetics models in generating simulations of locomotion (*e.g.*, (1,16,31,34)); however, there usually has not been a strong focus on directly relating mechanics and energetics of individual muscles. Prime examples of the potential of this approach can be found in two recent studies on triceps surae tendon compliance (11,26). Lichtwark and Wilson (11) combined muscle models with experimental measurements to study medial gastrocnemius efficiency (ratio of muscle work to muscle heat+work) during walking and running in humans. The measured stiffness of the Achilles tendon was found to be nearly optimal for maximizing gastrocnemius efficiency for both walking and running because of favorable fascicle shortening velocities in both gait forms. Sellers *et al.* (26) used a whole-body musculoskeletal model to generate energy-optimal simulations of running and found that the beneficial effects of storage and recovery of elastic energy on both speed and economy were due mostly to the mechanical properties of the Achilles tendon, with all other muscles combined making a smaller contribution. These studies reinforce the notion that the human Achilles tendon is a critical elastic energy store that is highly tuned to benefit both force production and energy consumption in locomotion.

Blood flow analyses in guinea fowl also have provided important insights into the links between muscle force, work, and energy use. Rubenson and Marsh (24) recently combined, for the first time, an inverse dynamic analysis with muscle blood flow and organismal energetics to assess the mechanical efficiency (ratio of mechanical power to metabolic power) of both the combined limb-swing muscles and a single limb-swing muscle (tibialis cranialis, an ankle flexor muscle). For both the combined limb-swing muscles (Fig. 6) and the tibialis cranialis, efficiency was quite low for walking (<5%) and increased considerably with speed. This led to the conclusion that the

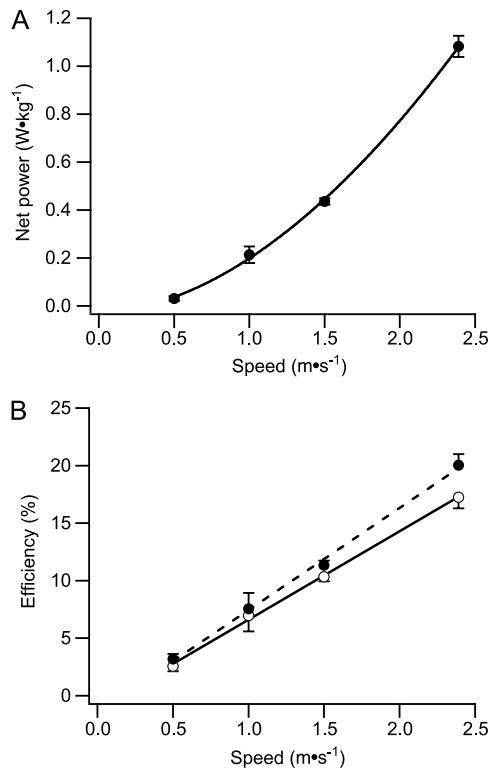


Figure 6. Efficiency of limb swing in guinea fowl. A. Average body mass-specific net mechanical power of limb swing as a function of speed (\pm SE), determined from inverse dynamics-based joint powers. Average mechanical power increased nearly quadratically with speed (velocity exponent = 1.83). B. Mechanical efficiency of limb swing as a function of speed (\pm SE). Positive efficiency (solid line) and absolute efficiency (after removing the estimated cost of absorbing work; dashed line) increased linearly with speed ($r^2 = 0.99$). [Adapted from Rubenson J, Marsh RL. Mechanical efficiency of limb swing during walking and running in guinea fowl (*Numida meleagris*). *J. Appl. Physiol.* 2009; 106:1618–30. Copyright © 2009 The American Physiological Society. Used with permission.]

mechanical work required to accelerate the limb was likely not the major determinant of energy use, except possibly at fast running speeds. Other mechanical functions, such as work done against antagonist muscles or isometric force production, also may be important determinants of limb-swing energy use (3,24). The efforts to assess efficiency of gastrocnemius (11) and tibialis cranialis (24) *in vivo* provide good examples of investigating the energetic function of an individual muscle with respect to its mechanical role (exit point C in Fig. 1).

Although the estimates of muscle efficiency described in the preceding paragraph were based on individual muscle energy use, the assessment of muscle-specific force and work was limited. Measurements of individual muscle force and work are possible in animal studies (e.g., (2)), and there have been some limited applications in humans (e.g., (8)). Buckle transducers, strain gauges, and fiber optic cables have been used to directly measure tendon forces, whereas sonomicrometry crystals attached to fascicles and ultrasonography have been adopted to assess muscle strain. These techniques have contributed substantially to our understanding of the mechanics of muscle function in locomotion, such as how fascicles and tendons interact with different muscle architectures, and under different locomotor conditions (2,8). We see future studies

pairing direct muscle force and work measurements with data on muscle blood flow as a powerful approach for linking the mechanics and energetics of locomotion at the muscular level. However, direct simultaneous measurements of muscle force and energy use likely will be limited to animal studies for the near future. Although measurement of tendon force in humans is possible, blood flow is difficult to measure in humans during gait and is restricted to certain muscles, leaving the modeling approach as the best available option.

CHALLENGES FOR THE FUTURE

Estimates of energy use in individual muscles have revealed much about the energetics of locomotion, yet there is still some uncertainty when associating energy consumption with the specific functions performed by muscles. For example, some muscles described earlier in the article as “hip extensors” or “knee extensors” actually exert force across more than one joint, and muscles, in general, may have more than one simultaneous function. The latter issue creates a complication with determining how much of the cost of locomotion is due to generating force versus performing work. Muscles can generate force with or without performing work; however, a muscle cannot perform work without also generating force. In the case where a muscle simultaneously generates force and performs work, it is not obvious how the metabolic energy consumed by the muscle should be partitioned between these two functions. Even in the case where a muscle performs no work, interpretation can be difficult, as an isometric muscle can potentially contribute simultaneously to supporting the body against gravity, propelling the body forward, increasing the mechanical energy of some body segments, and decreasing the mechanical energy of others (36). Thus, even when individual muscle energy consumption, force, and work can be readily quantified, attributing energy use to different functions remains a challenge.

In addition to these conceptual issues, there are other more practical matters to consider. The muscle blood flow technique is technically challenging, and accurate results depend on a number of factors. In particular, the injected microspheres must be well mixed in the blood, and an accurate reference blood withdrawal is critical. Moreover, the number of injected spheres must be low enough so as not to compromise the circulation, while still allowing an adequate number of spheres to be recovered in each tissue (13). With proper procedures, measurement of blood flow is possible in all muscle tissues; however, measuring muscle force and work *in vivo* is restricted to a few superficial muscles that are amenable to instrumentation. An integrated understanding of the energetic function of all muscles is therefore not possible with an experimental approach alone. The modeling approach also has important limitations. Although the muscle energetics model used in the research highlighted here (33) has been shown to yield good predictions of net and/or gross cost for walking, running, and pedaling (16,31,33,34), there is an inherent difficulty in validating the individual-muscle predictions that are of primary interest. More thorough validation of model-predicted muscle force and energy use for *in vivo* conditions will be needed to enhance the usefulness of musculoskeletal

modeling as a scientific tool for studying locomotor energetics. We propose a hybrid approach, whereby the wealth of *in vivo* muscle mechanics and muscle energy data available from animal studies are combined with species-specific musculoskeletal models, which will allow for a degree of model validation not usually possible. At the same time, every effort should be made to improve the predictive capacity of muscle models in humans, using the ever-growing suite of noninvasive and minimally-invasive means for characterizing muscle performance *in vivo*. Sonographic measures of blood flow, near-infrared spectroscopy, or ^{31}P magnetic resonance spectroscopy can be used to estimate muscle energy consumption, whereas ultrasonography can be used to measure fascicle and tendon strain, and fiber optics or intramuscular pressure measurements can provide estimates of muscle or tendon forces. Together, these efforts will lead to refined models and experimental procedures that will permit specific hypotheses regarding the energetics of locomotion to be tested across all muscles. Such an integrated framework will pave the way for human studies addressing both healthy and impaired gait and comparative studies seeking to identify the general principle of locomotion.

SUMMARY

Unraveling the energetic function of muscle is central to our basic understanding of terrestrial locomotion and has important implications for the evaluation and treatment of many gait disorders. The combination of organismal energy consumption with other markers of locomotor performance continues to advance our knowledge of locomotor energetics. Combining organismal energy consumption with estimates of energy use in individual muscles is an especially promising path for improving our understanding of locomotor energetics. Musculoskeletal modeling and muscle blood flow techniques currently provide the best means for estimating muscle energy use during locomotion, yet each of these techniques has its own set of limitations. Future efforts to integrate these two approaches hold great promise for accelerating our understanding of muscle function in locomotion.

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