Powering locomotion? It’s a loaded question

MUSCLES ARE THE MOTORS that power our movements, and, like all motors, muscles consume energy to carry out these actions. Quantifying the efficiency of locomotion (i.e., the mechanical power output divided by the metabolic power input) is the standard approach for relating the mechanics and energetics of movement. However, this approach is problematic when applied to legged locomotion such as walking and running because during these activities muscles are also active as brakes and isometric struts (2). Several recent studies, including one published by McGowan et al. (11) in the October issue (vol 101: 1060–1069) of the Journal of Applied Physiology, set the stage for major advances in our understanding of the causal relationship between in vivo muscle dynamics and the metabolic cost of locomotion.

These studies took advantage of one of the classic ways of experimentally manipulating the biomechanics and energetics of locomotion: load carrying. Previous load-carrying studies have led to the discovery of fantastic physiological feats, such as the inexpensive and exceptional load-carrying capabilities of some African head-load carrying women (8), Nepalese porters (1), and rhinoceros beetles (7). In addition to revealing these physiological mysteries, the study of load carrying has inspired an alternative approach to relating the mechanics and energetics of locomotion.

In 1980, Taylor and colleagues (12) proposed that the cost of generating muscular force to support body weight was the primary determinant of the metabolic cost of running. This proposal was based on their observation that the metabolic cost of running with a trunk load increased in direct proportion to the weight of the load. Although this study could not differentiate between the metabolic costs associated with muscular work versus force generation, it inspired subsequent studies that have attempted to do so (4–6). One major limitation for all of these studies has been a lack of information about how muscles are active in vivo during load carrying. In the report by McGowan et al. (11), the authors provide new insight into the causal relationship between the mechanics and energetics of locomotion by showing how the contractile patterns of two major hindlimb extensor muscles of guinea fowl are altered by load-carrying exercise.

The authors tested the hypothesis that load carrying would reduce the metabolic cost of generating muscular force by decreasing extensor muscle shortening velocity and enhancing stretch activation. The authors directly measured the in vivo length behavior and activity of the iliotibialis lateralis pars postacetabularis (ILPO; a biarticular muscle with extensor actions at both the hip and knee) and the medial head of the gastrocnemius (MG; a monoarticular ankle extensor with a small knee extensor component) using sonomicrometry and fine-wire electromyography (EMG). They found that for both muscles, load carrying had no effect on muscle shortening velocities, but it enhanced the active stretch of the muscles, especially the ILPO, early in stance. This suggests that the metabolic cost of generating muscular force decreases with added load.

Does this apparent economy of muscular force generation during load carrying translate to economic whole body metabolism? At first glance it does. The authors show that the net metabolic rate only increased 17% for guinea fowl carrying a trunk load equal to 22% of body mass. However, this is where interpreting the authors’ results gets exciting, because guinea fowl are currently one of the best animal models for studying the relationship between the mechanics and energetics of locomotion. This is in large part due to recent work by Marsh and colleagues (e.g., 3, 9, 10). Using a microsphere technique to measure individual muscle blood flow as an indicator of the metabolic rate of individual muscles, Marsh et al. (9) found that ~25% of the net muscle blood flow in the hindlimbs of walking and running guinea fowl occurred in muscles that were primarily active during the swing phase. Thus stance limb muscle actions (i.e., those available to support added trunk loads) account for ~75% of the net metabolic rate during walking and running (9). Consequently, a 22% trunk load would be predicted to increase the net metabolic rate by 16.5%, almost exactly as observed (10, 11). This suggests that the inexpensive load carrying by guinea fowl is not due to economic force generation, but instead it can be explained by the relative costs of stance and swing muscle actions.

Inferring the relative costs of stance and swing muscle actions by comparing the change in whole body metabolic rate to the change in added load requires a number of assumptions about the contractile dynamics of the muscles that respond to the added load (6), some of which may be untenable (10). Fortunately, McGowan et al. (11) designed their experiment such that the speed and load-carrying conditions matched those of two recent studies by Marsh and colleagues (3, 10) on the organismal metabolism and individual muscle blood flow of trunk load carrying by guinea fowl. This provides the unique opportunity to make in vivo comparisons of loading-induced changes in muscle contractile dynamics and individual muscle metabolic energy use. In the case of the ILPO, the average EMG intensity increased 17% for the 22% body mass load (11). This less than proportional increase in muscle activity is consistent with the authors’ conclusion that load carrying enhanced passive force production by increasing active stretching of the ILPO early in the stance phase. The fractional increase in muscle blood flow to the ILPO was nearly the same as the average EMG intensity, ~18% (3), which was also satisfyingly similar to the percent increase in organismal metabolism. However, the comparisons were not so tidy for the MG, as the average EMG intensity increased 27% during load carrying (11), whereas the fractional increase in blood flow to the MG only increased by ~6% (3).

These comparisons highlight the difficulty in interpreting the relationship between in vivo muscle contractile data and energy use. The close match between ILPO muscle activity and blood flow—and the less than proportional changes in muscle activity and blood flow compared with the added load—suggest that enhanced economic force generation due to active stretching may offset other factors predicted to increase the metabolic cost of generating force, such as changes in fiber type usage with increased force production (10). However, the disconnect between MG blood flow and EMG activity indicates that a causal relationship between these two variables should be interpreted cautiously. Information about muscle force levels would likely improve the comparison by allowing...
the time-integrated muscle force levels or work rates to be calculated. Additional measurements of the muscle mechanical advantage would be needed to determine how specific muscles contribute to supporting the added mass. With those data in hand, it would be possible to begin to understand the relative mechanical and metabolic roles of muscles designed for producing work (e.g., ILPO) versus generating force (e.g., MG) in responding to the added demand of load carrying. Despite the current uncertainties, the groundwork is being laid for an exciting future in which in vivo muscle biomechanics and metabolism are integrated during complex behaviors such as walking and running.

REFERENCES


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