

Exoskeletons Improve Locomotion Economy by Reducing Active Muscle Volume

Owen N. Beck^{1,2}, Laksh Kumar Punith¹, Richard W. Nuckols^{3,4}, and Gregory S. Sawicki^{1,2}

¹The George W. Woodruff School of Mechanical Engineering, ²School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA; ³Harvard John A. Paulson School of Engineering and Applied Sciences, Cambridge; and ⁴Wyss Institute for Biologically Inspired Engineering, Boston, MA

BECK, O.N., L.K. PUNITH, R.W. NUCKOLS, and G.S. SAWICKI. Exoskeletons improve locomotion economy by reducing active muscle volume. *Exerc. Sport Sci. Rev.*, Vol. 47, No. 4, pp. 237–245, 2019. Exoskeletons that improve locomotion economy typically are engineered to reduce users' limb joint mechanical work or moments. Yet, limb joint dynamics do not necessarily reflect muscle dynamics, which dictate whole-body metabolic energy expenditure. Here, we hypothesize that exoskeletons primarily reduce user metabolic energy expenditure across locomotion conditions by reducing active muscle volume. **Key Words:** energetics, metabolism, augment, locomotion, performance, biomechanics, assistive device

Key Points

- Center of mass, limb joint, and muscle mechanical do not explain well how exoskeletons alter locomotion economy.
- Limb joint dynamics do not necessarily reflect the underlying muscle dynamics across locomotion conditions.
- Active muscles are the primary drivers of whole-body metabolic energy expenditure during locomotion. Consequently, exoskeletons likely need to consider muscle dynamics to optimize locomotion economy.
- During walking and hopping with an exoskeleton, muscle force generation is a better correlate to locomotion economy than previously measured mechanical work parameters.
- Tracking muscle length changes *in vivo* may help provide reasonably accurate active muscle volume calculations.
- Future exoskeleton controllers may incorporate real-time muscle physiology measures to update device characteristics and maintain minimal active muscle volume and metabolic energy expenditure across locomotion conditions.

INTRODUCTION

Exoskeletons are wearable devices that are engineered to augment human locomotor performance by altering limb joint

dynamics. Popular culture often portrays exoskeletons as powerful devices that enable superhuman feats, such as outrunning automobiles and flying in outer space *à la* Marvel's Iron Man. In reality, exoskeletons do not yet enable humans to outrun automobiles or fly. However, assistive technology has progressed over the last decade, evidenced by the emergence of research-quality exoskeletons that reduce their users' metabolic energy expenditure (improve locomotion economy) versus using no device. In 2009, Sawicki and Ferris (1) were the first to report that an exoskeleton improved participant walking economy (with artificially long steps) compared with not using the device. Fast forward 10 yr, there are now numerous autonomous exoskeletons spanning multiple designs that have been reported to reduce user metabolic energy expenditure during natural walking and running. Although exoskeletons will never fulfill Hollywood's fantasies, assistive device technology is inching closer to minimizing user metabolic energy expenditure and augmenting human locomotion throughout everyday life.

To optimize user locomotion economy across real-world conditions (*e.g.*, across modes, speeds, ground slopes, terrain), it is essential for exoskeletons to target biomechanical parameters that directly influence metabolic energy expenditure. Today, nearly all exoskeletons are engineered to improve locomotion economy by altering a single biomechanical parameter, typically reducing the users' limb joint mechanical work (2–4) or moment (2,4,5). Although targeting a single biomechanical parameter oversimplifies the relation between human movement and metabolic energy expenditure, it provides a tractable approach for designing exoskeletons. Furthermore, regardless of the design, it is unestablished how exoskeletons fundamentally alter user biomechanics to reduce metabolic energy expenditure. Irrespective of how exoskeletons alter user limb joint biomechanics, they may actually improve locomotion economy by indirectly changing muscle-level parameters.

Address for correspondence: Owen N. Beck, School of Mechanical Engineering, Georgia Institute of Technology, 455 Callaway Manufacturing Research Center Building, 813 Ferst Drive NW, Atlanta, GA 30332 (E-mail: obeck3@gatech.edu).

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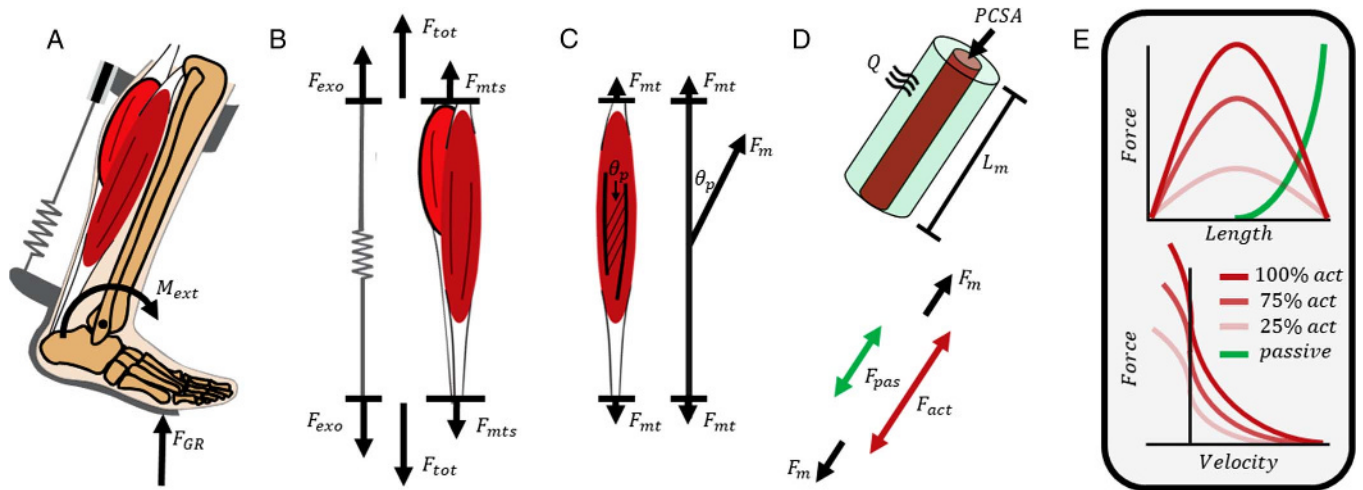


Figure 1. Illustration of the key factors that enable the calculation of active muscle volume. A. Leg with an ankle exoskeleton in parallel to the ankle joint. Ground reaction force (F_{GR}) and ankle joint extension moment (M_{ext}). B. Diagram of the force acting on the exoskeleton (F_{exo}) and triceps surae muscle-tendons (F_{mts}). C. The force on the soleus muscle-tendon (F_{mt}), soleus fascicle pennation angle (θ_p), and muscle fascicle force (F_m). D. Active muscle (red cylinder); passive muscle (light green cylinder); heat liberation (Q); physiological cross-sectional area (PCSA); muscle length (L_m), and passive (F_{pas}), active (F_{act}), and total muscle force (F_m). E. Top: Muscle's force-length relations. Bottom: Muscle's force-velocity relations. Green indicates passive; dark red, 100% activation (act); medium red, 75% activation; and light red, 25% activation.

The purpose of this review is to pose a novel hypothesis regarding how exoskeletons improve locomotion economy. Ultimately, active skeletal muscles are the primary consumers of metabolic energy during locomotion (6), and their contractile dynamics govern their metabolic energy expenditure (7–10). Furthermore, most of muscle's metabolic energy expenditure occurs to cycle actin-myosin cross-bridges (8,10). Accordingly, we hypothesize that exoskeletons primarily reduce whole-body metabolic energy expenditure by decreasing the volume of muscle that is actively cycling actin-myosin cross-bridges (Fig. 1). Using inverse dynamics, musculoskeletal imaging, anatomical measures, muscle models, and a few assumptions, researchers can estimate active muscle volume during exoskeleton-assisted locomotion. In addition, because of the disassociation between limb joint and muscle dynamics (11–13), we posit that exoskeletons need to assess and target muscle, not limb joint, dynamics to minimize active muscle volume across locomotion conditions.

To do this, exoskeletons may begin incorporating techniques to monitor user muscle physiology in real time, enabling devices to update parameters (e.g., exoskeleton stiffness) and maintain a minimal volume of active muscle across tasks (Fig. 2). Until refuted, this hypothesis may serve as a roadmap to enhanced exoskeleton design by revealing the biomechanical parameter that best links device-altered biomechanics to metabolic energy expenditure.

MUSCLES ARE THE PRIMARY CONSUMERS OF METABOLIC ENERGY DURING LOCOMOTION

The notion that active muscles govern locomotion economy is supported by studies that track systemic blood flow (6). To review, arterial blood flow transports oxygen to active muscles, where its presence helps convert macronutrients to usable energy packets (adenosine triphosphate (ATP)) needed for muscle contraction (14). One such study reported that ~90% of

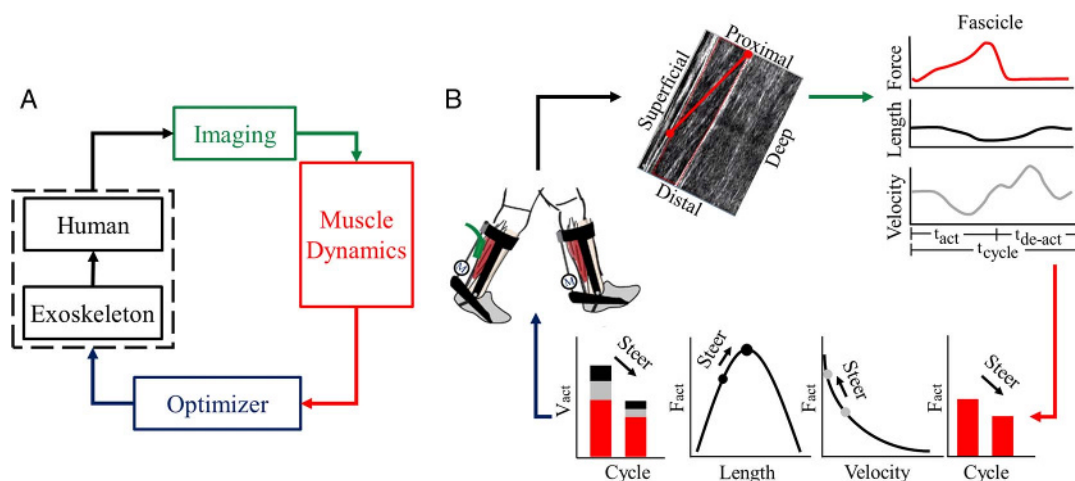


Figure 2. Steering muscle dynamics in the loop. A. Diagram demonstrating an exoskeleton controller that incorporates real-time muscle imaging measures to optimize device characteristics. B. An exoskeleton that optimizes muscle dynamics by tracking muscle fascicle lengths and velocities then updates its controller to shift muscle length and velocity to reduce active muscle volume (V_{act}).

guinea fowl's increased cardiac output across walking and running speeds is directed to active leg muscles (15,16). In addition, during human cycling, oxygen delivery to active leg muscles almost directly reflects changes in whole-body oxygen uptake across relative aerobic intensities (20% to 100% $\dot{V}O_{2max}$) (17,18). Consequently, devices designed to alter biomechanics, such as exoskeletons, ultimately improve locomotion economy by changing muscle dynamics.

CONVENTIONAL WISDOM: LINKING BIOMECHANICS TO METABOLIC ENERGY EXPENDITURE

A person's metabolic energy expenditure equals his or her heat liberation plus net mechanical work production (14,19). Because of the difficulty of measuring heat liberation (14), researchers often relate only a person's mechanical work production to his or her metabolic energy expenditure (20–22). However, net mechanical work during level-ground constant-speed locomotion is approximately zero, whereas a person's rate of metabolic energy expenditure via aerobic metabolism can reach over 2000 W (23,24). Thus, to relate mechanical work to metabolic energy expenditure, researchers often scale the efficiencies of positive and negative mechanical work (25) or ignore the negative mechanical work production (20).

Center of Mass Mechanical Work

Over each stride (one stride comprises two steps), a person performs gross positive and negative mechanical work by raising, lowering, accelerating, and decelerating his or her center of mass (CoM) (20,22,25,26). Positive CoM mechanical work (*i.e.*, external work) is often computed by researchers to help explain the corresponding metabolic energy expenditure (22,26). However, does CoM mechanical work describe how exoskeletons alter locomotion economy? To answer this question, we highlight the results from an exoskeleton-assisted hopping study (27). Occasionally, researchers test their walking and running exoskeleton prototypes during human hopping (13,27). The fundamental stance phase biomechanics of walking, running, and hopping are all well characterized by a spring-mass model (28,29), and hopping enables researchers to test their prototypes before dealing with swing phase mechanics. Specifically, Grabowski and Herr (27) developed a full-leg passive exoskeleton and tested the influence of its stiffness on user CoM dynamics and metabolic energy expenditure during hopping (Fig. 3). At matched hopping frequencies, the stiffer exoskeleton reduced biological positive CoM mechanical work by ~18% to 40% compared with the more compliant exoskeleton while requiring 20% to 35% more metabolic energy (Fig. 3). These results suggest that CoM mechanical work does not correspond to metabolic energy expenditure during exoskeleton-assisted movement.

Limb Joint Mechanical Work

Perhaps CoM mechanical work does not provide enough resolution to link biomechanics to metabolic energy expenditure. For instance, many hip, knee, and ankle joint mechanical work profiles can yield the same gross positive and negative CoM mechanical work per cycle (30). Adopting more flexed limb joint postures during locomotion typically increases the limb joint moments by decreasing the corresponding effective mechanical advantages (31,32). Thus, while sweeping a constant angular

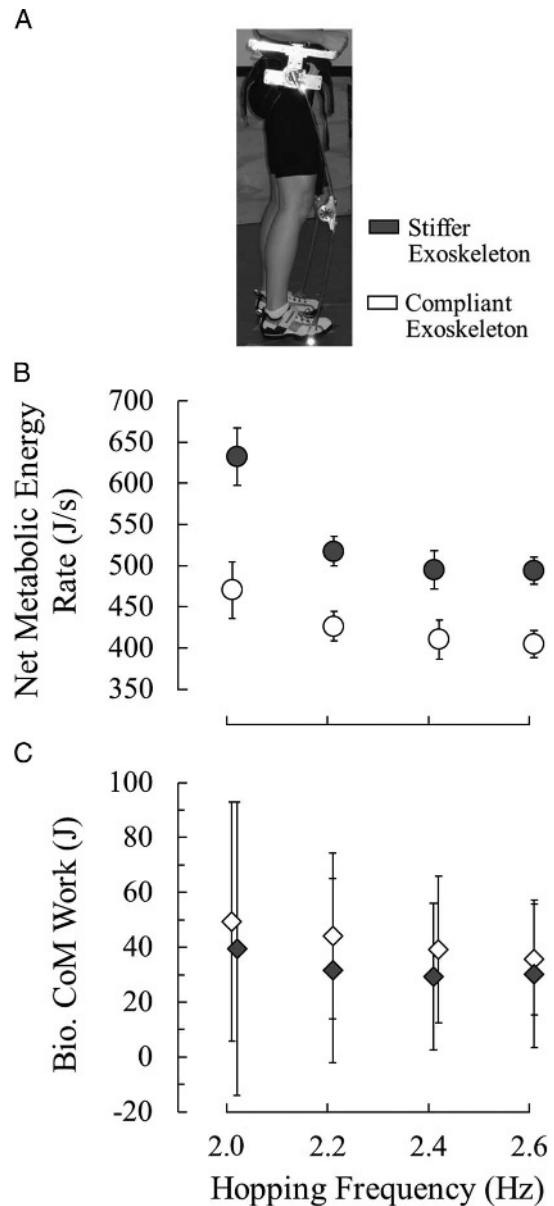


Figure 3. A. Grabowski and Herr's (27) exoskeleton worn by a participant. B. Average rate of net metabolic energy expenditure during hopping with the stiffer (gray symbols) and compliant (open symbols) exoskeletons at different frequencies. C. The biological contribution to the positive center of mass (CoM) mechanical work per hop with the stiffer and more compliant exoskeletons at different frequencies. Error bars indicate standard error (SE). [Adapted from Grabowski AM, Herr HM. Leg exoskeleton reduces the metabolic cost of human hopping. *J. Appl. Physiol.* 2009; 107:670–678. Copyright © 2009 The American Physiological Society. Used with permission.]

displacement, more flexed limb joint postures (*e.g.*, (33)) may yield greater gross mechanical limb joint mechanical work while maintaining similar relative CoM mechanical energy fluctuations. Because of the disconnect between limb joint and CoM dynamics (11–13), limb joint mechanical work may more directly link exoskeleton-assisted movement to the respective whole-body metabolic energy expenditure.

Modern exoskeletons are often engineered to improve locomotion economy by reducing limb joint positive mechanical work (2–4). Although this device design has improved locomotion economy versus not using a device (3,34,35), these exoskeletons

are not directly designed to target the mechanism(s) governing metabolic energy expenditure. This statement is supported by the study of Farris and Sawicki (13), which involved participants hopping with and without an ankle exoskeleton. Explicitly, they reported that while participants hopped at 3.2 Hz, an ankle exoskeleton reduced the average user positive biological ankle joint mechanical work rate by ~29% while requiring ~12% more metabolic energy expenditure compared with using no device (13). Further evidence is presented by Collins *et al.* (5), whose ankle exoskeleton stiffness condition that minimized user positive biological ankle joint mechanical work rate (power) during walking at 1.25 m·s⁻¹ required the numerically greatest rate of metabolic energy expenditure (Fig. 4). Lastly, compared with not using a device, passive exoskeletons have improved locomotion economy while requiring biological leg joints to perform *more* net mechanical work (5,36), through imperfect user-device interfaces and adding nonideal springs to the legs (*i.e.*, adding sources of mechanical energy dissipation to the body). Hence, reducing biological limb joint mechanical work does not describe how exoskeletons improve locomotion economy.

Limb Joint Moments

As an alternative to the mechanical work/efficiency approach, muscle force generation may explain how exoskeletons alter locomotion economy. After all, isometric muscle contractions require metabolic energy to generate force (8). In 1980, Taylor *et al.* (37) proposed that muscle force generation drives locomotion economy after realizing that mass-specific mechanical work does not correspond to mass-specific running economy measures across animal sizes (22). Since that proposal, many locomotion studies have incorporated limb joint moments to help explain how biomechanics affect locomotion economy (38,39). Yet, ankle joint moments during hopping (13) and walking (5) with and without an ankle exoskeleton cannot explain the metabolic energy expenditure during the respective tasks. For example, Collins *et al.* (5) reported that an ankle exoskeleton yielded the numerically worst walking economy condition when the ankle joint moment rate was the least (Fig. 4). Therefore, neither limb joint mechanical work nor moment can reliably explain how exoskeletons alter user metabolic energy expenditure.

DECOUPLING OF LIMB JOINT AND MUSCLE DYNAMICS

Perhaps neither CoM nor limb joint biomechanical parameters explain the exoskeleton-altered metabolic energy expenditure changes because they do not well characterize the underlying muscle dynamics. Many anatomical factors decouple limb joint and muscle dynamics. This is apparent during the initial ~50% of the stance phase of walking and running, because the ankle joint performs net negative mechanical work (30,40) while the triceps surae muscles generate force but perform roughly zero mechanical work during walking (41) and net positive mechanical work during running (42). In addition, neither the contracting muscles' line of action (43) nor mechanical advantage (44) is directly proportional to the respective limb joint dynamics throughout locomotion, indicating that the patterns of muscle mechanical work and force may change relative to the corresponding limb joint mechanical work and moment profiles. Furthermore,

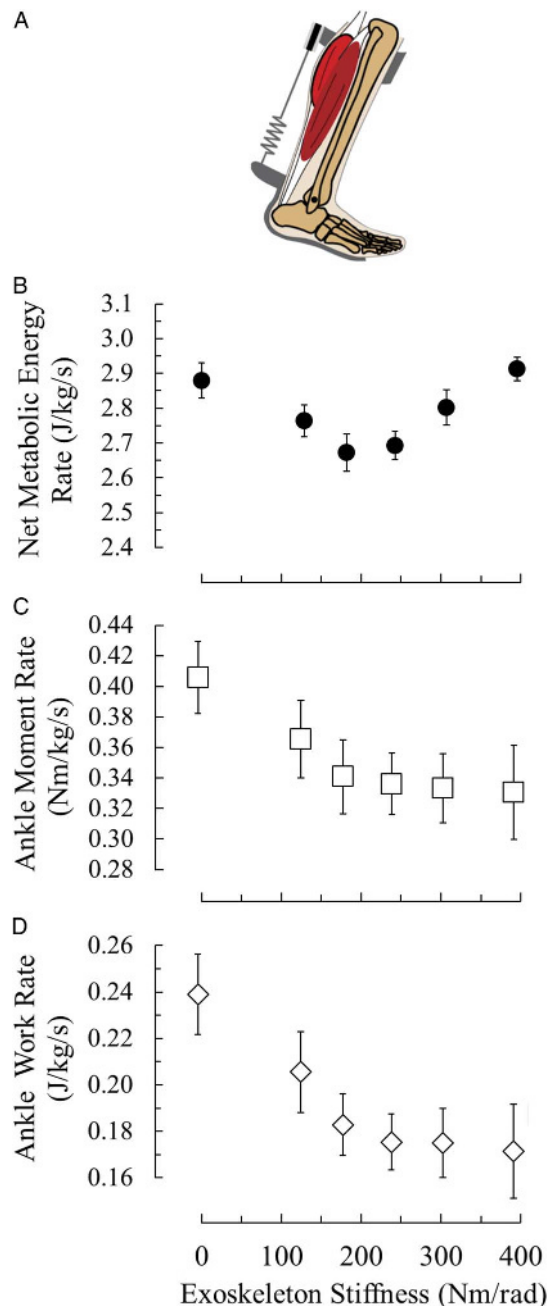


Figure 4. A. Representation of a walking leg using the autonomous ankle exoskeleton of Collins *et al.* (5). B. Rate of net metabolic energy expenditure (B), biological ankle moment rate (C), and biological ankle mechanical power (D) during walking at 1.25 m·s⁻¹ versus ankle exoskeleton stiffness. Error bars indicate standard error (SE). We used images and data from (5). [Adapted from Collins SH, Wiggin MB, Sawicki GS. Reducing the energy cost of human walking using an unpowered exoskeleton. *Nature* 2015; 522:212. Copyright © 2015 Springer Nature. Used with permission.]

multiple muscles contribute to limb joint dynamics, and biarticular muscles can transfer mechanical energy between limb joints, both of which make it difficult for joint-level calculations to accurately reflect the corresponding muscle dynamics. Thus, directly assessing muscle dynamics may be warranted to reveal the link(s) between exoskeleton-altered biomechanics and metabolic energy expenditure.

INSIGHTS FROM MUSCULOSKELETAL IMAGING

Musculoskeletal imaging techniques may help reveal how exoskeletons alter muscle dynamics and improve locomotion economy. With modern tools, researchers can noninvasively estimate muscle fascicle dynamics *in vivo* (11,12,42,43,45,46). To date, only a few experiments have incorporated muscle imaging techniques to help determine how wearable devices affect muscle dynamics and metabolic energy expenditure. After Farris and Sawicki (13) conducted limb joint analyses, they incorporated ultrasonography to further their knowledge regarding how a bilateral ankle exoskeleton affects soleus fascicle dynamics and relates to metabolic energy expenditure during hopping at 2.5 Hz (11). Compared with hopping without assistance, the ankle exoskeleton reduced positive biological ankle joint mechanical work by ~30%, yet positive soleus mechanical work was unaffected (11). Furthermore, the ankle exoskeleton reduced the soleus' rate of force generation by ~53% and the net metabolic rate by 19% versus hopping without assistance (11). Using similar experimental techniques, Takahashi *et al.* (43) measured soleus fascicle dynamics and metabolic energy expenditure while participants walked in custom footwear over a range of three-point bending stiffness values. The stiffest footwear condition increased soleus force generation by 9%, decreased positive soleus mechanical work production by 16%, and increased net metabolic energy expenditure by 11%, compared with the least stiff footwear (Fig. 5) (43). Together, these experimental studies (11,43) demonstrate the disconnect between limb joint and muscle dynamics while suggesting that muscle force is the best correlate (of the mentioned parameters) to metabolic energy expenditure during hopping and walking with an assistive device (Fig. 5). Importantly, muscle force generation is enabled by molecular processes that perform mechanical work (*e.g.*, actin-myosin cross-bridge cycling) and liberate heat, thereby coinciding with the laws of thermodynamics (14). Until researchers can quantify these infinitesimal mechanical work measures during exoskeleton-assisted human movement, we propose that estimating the heat and mechanical work generated by muscle “force” production is the best correlate to locomotion economy.

The aforementioned studies (11,43) quantified the dynamics of a single soleus fascicle and generalized them to whole-body metabolic energy expenditure. Obviously, one soleus fascicle does not govern whole-body metabolic energy expenditure during walking and hopping. However, mid-muscle fascicle measures are representative of fascicle length changes along the muscle (42) and positively correlated with the respective sarcomere length changes ($r = 0.67$) (47). In addition, the soleus is presumably one of the body's most metabolically active muscles during walking, running, and hopping due to the relatively large ankle joint moment (38,39), poor effective mechanical advantage (31), and relatively large physiological cross-sectional area (31). Moreover, ankle exoskeletons and custom footwear alter ankle muscle dynamics more than knee or hip muscle dynamics (11,43), indicating that the corresponding changes in metabolic energy expenditure are driven by the largest ankle muscle(s). Even though the view that ankle muscles expend more metabolic energy than knee and hip muscles during walking has not reached consensus (15), based on the implications of exoskeleton studies that related changes in soleus fascicle dynamics and metabolic energy expenditure, we move forward

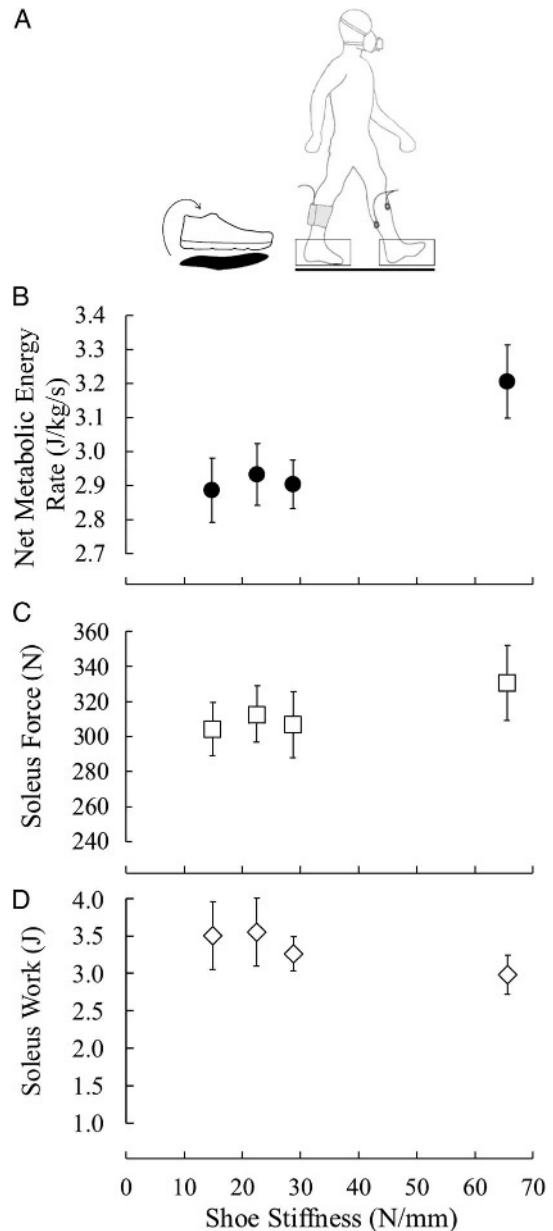


Figure 5. A. Depiction of an individual walking with custom footwear (43). B. Rate of net metabolic energy expenditure, and stride-averaged (C) soleus force and (D) soleus mechanical work during walking at $1.25 \text{ m}\cdot\text{s}^{-1}$ versus footwear three-point bending stiffness. Error bars indicate standard error (SE). This figure was created using images and data from (43) and is in accordance with the CC BY License. [Adapted from Takahashi KZ, Gross MT, van Werkhoven H, Piazza SJ, Sawicki GS. Adding stiffness to the foot modulates soleus force-velocity behaviour during human walking. *Sci. Rep.* 2016; 6:29870. Creative Commons Attribution 4.0 International Public License.]

with the notion that device-altered locomotion economy is best explained by muscle force generation.

RELATING ACTIVE MUSCLE VOLUME TO METABOLIC ENERGY EXPENDITURE

The metabolic energy expended to generate a unit of muscle force primarily depends on the active actin-myosin cross-bridges ($\geq 60\%$ to 70% of ATP use is due to actin-myosin ATPase activity (8,10,48)). This is because the cross-sectional

area of an active muscle is proportional to active muscle force (49,50), and directly cycling the actin-myosin cross-bridges of a muscle constitutes the majority of its metabolic energy expenditure (8,10). Furthermore, anatomical uniformities enable researchers to estimate the number of actin-myosin cross-bridge cycles per unit active muscle force. For example, actin and myosin filament dimensions as well as the number of cross-bridges per sarcomere are fairly consistent across striated muscles (50,51). Thus, while considering other parameters, the number of active actin-myosin cross-bridges is directly proportional to muscle fiber length (49,50) (Fig. 1). In other words, activating longer muscles yields more active actin-myosin cross-bridges and expends more metabolic energy than shorter muscles. Hence, extending muscle force measures to the volume of active muscle necessary to sustain locomotion should theoretically improve the ability of researchers to link exoskeleton-altered biomechanics and locomotion economy.

Next, we detail how to calculate active muscle volume (*i.e.*, the volume of muscle with active actin-myosin cross-bridges) and relate it to metabolic energy expenditure during walking for a leg extensor muscle that is active during ground contact and passive during leg swing. This approach can be used for all muscles. During the ground contact phase of locomotion, external (*e.g.*, ground reaction forces) and internal (*e.g.*, antagonist muscle-tendon forces) forces yield moments that flex the ankle, knee, and hip joints (31). To prevent the leg joints from collapsing under these moments, extensor muscles must generate force, which is transmitted by tendons, to oppose the corresponding joint flexion moments (equation 1) (31). Without an exoskeleton, extensor muscle-tendons produce biological joint moments (M_{bio}) that are equal and opposite to the external (M_{ext}) and internal (M_{int}) flexor joint moments per stride. Exoskeletons can and have been reported (2,4,5,13) to decrease biological joint extensor moments by applying an extensor torque about the target joint (τ_{exo}) (Figs. 1 and 2).

$$M_{\text{bio}} = M_{\text{ext}} + M_{\text{int}} - \tau_{\text{exo}} \quad [\text{Eq. 1}]$$

Multiple muscle-tendons contribute to each limb joint's extension moment (Fig. 1) (31). To estimate the contribution of each muscle-tendon to its respective biological joint moment, we assume that muscle-tendons contribute a limb joint extensor moment (M_{mt}) that is proportional to its muscle's physiological cross-sectional area (PCSA_{m}) divided by the total biological joint extensor's physiological cross-sectional area (PCSA_{bio}) (31,38,39,49).

$$M_{\text{mt}} = M_{\text{bio}} \cdot \frac{\text{PCSA}_{\text{m}}}{\text{PCSA}_{\text{bio}}} \quad [\text{Eq. 2}]$$

Extensor muscle-tendon force (F_{mt}) equals the quotient of the corresponding muscle-tendon moment (M_{mt}) and its moment arm length (r_{mt}) (31,38,39,49).

$$F_{\text{mt}} = \frac{M_{\text{mt}}}{r_{\text{mt}}} \quad [\text{Eq. 3}]$$

By deeming that muscles consume all of the muscle-tendon's metabolic energy expenditure, we solved for muscle force

(F_{m}) by considering the muscle fiber pennation angle ($\cos \theta_{\text{p}}$) (Fig. 1).

$$F_{\text{m}} = \frac{F_{\text{mt}}}{\cos \theta_{\text{p}}} \quad [\text{Eq. 4}]$$

Moreover, muscles generate force passively when they are stretched beyond their resting lengths (52). Thus, we subtract passive muscle force (F_{pas}) from total muscle force (F_{m}) to calculate active muscle force (F_{act}) (Fig. 1).

$$F_{\text{act}} = F_{\text{m}} - F_{\text{pas}} \quad [\text{Eq. 5}]$$

Furthermore, muscle metabolic energy expenditure depends on active muscle force (8), operating length (9), and contractile velocity (7). Accordingly, we accounted for these parameters by adopting a "Hill-type muscle model" to compute active muscle force using maximum isometric force (F_{max}) and scaling factors to represent relative activation (*act*), as well as the influence of the force-length (FL) and force-velocity (FV) relations (53).

$$F_{\text{act}} = F_{\text{max}} \cdot \text{act} \cdot \text{FL} \cdot \text{FV} \quad [\text{Eq. 6}]$$

A muscle's maximum isometric force is the product of the corresponding specific tension (σ) and total muscle volume (V_{tot}) divided by fascicle length (l_{m}).

$$F_{\text{max}} = \sigma \cdot \frac{V_{\text{tot}}}{l_{\text{m}}} \quad [\text{Eq. 7}]$$

By substituting equation 7 into equation 6, we can express active muscle force (equation 8):

$$F_{\text{act}} = \sigma \cdot \frac{V_{\text{tot}}}{l_{\text{m}}} \cdot \text{act} \cdot \text{FL} \cdot \text{FV} \quad [\text{Eq. 8}]$$

Rearranging equation 8 allows us to compute active muscle volume (V_{act}), which is the product of relative muscle activation (*act*) and total muscle volume (V_{tot}).

$$V_{\text{act}} = V_{\text{tot}} \cdot \text{act} = \frac{F_{\text{act}} \cdot l_{\text{m}}}{\sigma \cdot \text{FL} \cdot \text{FV}} \quad [\text{Eq. 9}]$$

Next, we can relate active muscle volume to the rate of metabolic energy expenditure (metabolic power, \dot{E}_{met}),

$$\dot{E}_{\text{met}} = \dot{P}_{\rho} \cdot V_{\text{act}} \quad [\text{Eq. 10}]$$

where \dot{P}_{ρ} is the muscle's metabolic power density, which is its rate of metabolic energy expenditure per unit active muscle volume ($\text{J} \cdot \text{cm}^{-3} \cdot \text{s}^{-1}$).

Locomotion economy is typically expressed as the average rate of metabolic energy expenditure over numerous cycles (*e.g.*, stride and hops). Thus, to link our biomechanical parameters to an average rate of metabolic energy expenditure, we integrate and divide as per equation 11. t_0 and t_{end} correspond to a task's initial and final times, respectively.

$$\dot{\bar{E}}_{\text{met}} = \frac{\int_{t_0}^{t_{\text{end}}} (\dot{P}_{\rho} \cdot V_{\text{act}}) dt}{t_{\text{end}} - t_0} \quad [\text{Eq. 11}]$$

Lastly, for a task that requires more than one muscle (i), contributions from each muscle can be summed to determine whole-body metabolic energy expenditure ($\dot{\bar{E}}_{\text{met, body}}$).

$$\dot{\bar{E}}_{\text{met, body}} = \sum_{i=1}^n \frac{\int_{t_0}^{t_{\text{end}}} (\dot{P}_{\rho} \cdot V_{\text{act}})_i dt}{t_{\text{end}} - t_0} \quad [\text{Eq. 12}]$$

The ability to accurately implement equations 1–12 depends on researcher ingenuity and available resources. Nonetheless, researchers can determine active muscle volume using assumptions and many experimental techniques, including, but not limited to, inverse dynamics, magnetic resonance imaging (54), ultrasonography (44,55), sonomicrometry (56), cadaver data (31,57), dynamometry (55), and electromyography.

Extending Existing Force-Based Models

Our active muscle volume calculation is built on the foundation of the “cost of generating force hypothesis,” which was proposed and refined by Taylor, Kram, and colleagues (38,39,58). In the previous cost of force calculations, researchers also estimated the muscle volume needed to generate force (38,39,58). In this review, we extended the ability to estimate the relevant volume of muscle by, among other things, accounting for passive muscle force, pennation angle, and relative contractile muscle lengths and velocities (Fig. 1). By incorporating these measures, we may be able to better explain locomotion economy using assistive devices, as well as across multiple modes, ground slopes, and damped terrain — all of which have stifled traditional force-based models (59). Of note, our biomechanics to metabolic energy expenditure calculation is, in some ways, simpler than many force-based locomotion economy models because we do not include the rate of generating force (38,39,58). Furthermore, despite these advances in calculating active muscle volume, current force-length (60) and force-velocity (52) relations are developed from quasi-static measurements, which may not perfectly relate muscle activation with the transient muscle dynamics. In addition, we assume that the number of cross-bridges that are cycling is proportional to active muscle volume; however, the relation between the volume of muscle activated and the number of actively cycling cross-bridges (the primary source of metabolic energy expenditure) is mode and history dependent. Thus, although we expect that including Hill-type properties to the model better links biomechanics to locomotion economy than measurable force or work parameters *per se*, future research is warranted to establish how muscle force production during dynamic tasks affects metabolic energy expenditure.

APPLICATIONS AND FUTURE DIRECTIONS

Other Sources of Muscle Metabolic Energy Expenditure

The metabolic energy expended per skeletal muscle contraction also depends on factors that are not directly related to cross-bridge cycling (8,10,48). One such factor is the metabolic energy expended to pump ions. For example, during isometric contractions, ~30% to 40% of the muscle’s metabolic energy

is expended to pump Na^+ - K^+ and Ca^{2+} (8,10,48), with this relative cost decreasing with increased muscle shortening (61). Moreover, activating and deactivating muscles at faster rates generally require more metabolic energy, due to increased ion pumping (62–64), as well as the recruitment of faster, less efficient muscle fibers (65). Thus, although active muscle volume may be the primary factor driving metabolic energy expenditure, to fully link biomechanics to locomotion economy, it is necessary to consider all sources of ATP use.

The Next Exoskeleton Technologies

Although we are currently fixated on using exoskeletons to improve locomotion economy, assistive device technology has many avenues for augmenting user locomotion. To highlight a couple of possibilities, exoskeletons may be used to improve a user’s top speed by increasing muscle force capacity (66) or stability by enhancing the output of muscle proprioceptors. Regardless of the desired outcome, we expect that the next generation of exoskeletons may benefit from bringing physiology in the loop, perhaps by using musculoskeletal imaging to update device parameters in real time and maintain the desired muscle dynamics (Fig. 2). Developing autonomous exoskeletons that incorporate physiology in the loop will require innovation but, when successful, will augment human locomotion across tasks and environments that we navigate in the natural world.

CONCLUSIONS

The last decade witnessed the emergence of wearable exoskeletons that can improve human locomotion economy versus not using a device (3,5,36). Regardless of the exoskeleton design, we hypothesize that devices predominantly improve locomotion economy by reducing the user’s active muscle volume. Moving forward, active muscle volume may be a useful parameter to target when devising exoskeletons designed to improve locomotion economy, primarily because it is informed by time-tested, fundamental physiological principles that link individual muscle dynamics and whole-body metabolic energy expenditure.

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