ARTICLE

It Pays to Have a Spring in Your Step

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SAWICKI, G.S., C.L. LEWIS, and D.P. FERRIS. It pays to have a spring in your step. *Exerc. Sport Sci. Rev.*, Vol. 37, No. 3, pp. 130–138, 2009. *In humans, a large portion of the mechanical work required for walking comes from muscle-tendons crossing the ankle joint. Elastic energy storage and return in the Achilles tendon during each step enhance the efficiency of ankle muscle-tendon mechanical work far beyond what is possible for work performed by knee and hip joint muscle-tendons.*

Key Words: gait, locomotion, walking, energetics, exoskeleton, efficiency

INTRODUCTION

Human walking mechanics have long been described using an inverted pendulum analogy (5). The body center of mass travels in an arc trajectory such that it rises and decelerates during the first half of stance, and lowers and accelerates during the second half of stance, similar to an inverted pendulum. By coupling a regular pendulum to an inverted pendulum to make a swing leg and a stance leg, a simple passive model can reproduce the basic movement and energy patterns of human walking (15,20). Despite their simplicity, passive pendular models make a number of key predictions about the energetics of bipedal walking. First, energy can be conserved by exchanging kinetic and gravitational potential energy during the stance phase of each step. Second, leg swing can be purely passive under certain initial conditions. Third, the major source of energy loss during walking is the step-to-step transition (16). At this time, the center of mass must be redirected from moving downward and forward to moving upward and forward. This redirection requires mechanical work to maintain steady speed walking dynamics (16).

Simple models also provide insight into how the mechanical energy lost in the foot-ground collision is replaced by positive mechanical work performed by the legs. One way to perform the work is to generate an impulsive push-off along the trailing limb just before the leading limb collides with the ground. An alternative way to power level walking in the model is to use active hip torque (15). Either of these methods could be done solely with active power production or by supplementing active power production with recovered energy that was previously stored in elastic elements.

The potential benefits of elastic energy storage and return have been established for bouncing gaits such as hopping and running (1,5,14) but have received much less attention for walking gaits. It has often been accepted that longer stance times and asymmetric joint mechanical power outputs during walking limit the possibility for elastic energy storage and return by compliant tendons (2,12). This limitation has been challenged by recent walking models that extend the inverted pendulum concept by allowing the stance limb to compress and recoil (9). With the appropriate leg stiffness and initial conditions, a spring-loaded inverted pendulum model can generate walking dynamics that better match the trajectory of the center of mass (*i.e.*, a noncircular arc) and the double peak shape of the ground reaction force when compared with a rigid inverted pendulum model. Agreement between the spring-mass model and experimental walking data highlights the possibility that elastic energy storage and return may be important during walking. Although the positive mechanical work during level walking must ultimately come from skeletal muscle (*e.g.*, during gait initiation), once at steady speed, mechanical work can repeatedly be stored in and released from elastic tissues. Cycling strain energy in elastic tendons could significantly reduce the positive mechanical work required by skeletal muscle.

Inverse dynamics analyses can give insight into the relative sources of mechanical power generation by the lower limb muscle-tendons during human walking. Data indicate that healthy young humans generate an impulsive push-off (similar to that used in the simple model (15)) over the double-support phase of walking using a large ankle muscle-tendon power burst. In fact, for preferred walking speeds on level ground (1.2–1.5 $m \cdot s^{-1}$), the ankle joint produces 35% to

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45% of the summed ankle, knee, and hip positive mechanical work during each stride (24,25,29). When viewing the stance phase only, the ankle joint performs 60% (30 J out of 50 J) of the summed ankle, knee, and hip positive mechanical work (Fig. 1) (6). Preceding the positive work at push-off, there is a period of ankle joint negative work, a necessary precondition for elastic energy storage and return. Mechanical work may also be transferred to the ankle from muscle-tendons at more proximal joints (*e.g.*, knee and hip) via biarticular linkages (*e.g.*, gastrocnemius or rectus femoris). In this case, mechanical work performed at other joints could be stored as elastic energy in the Achilles tendon.

Ultrasound imaging has allowed for quantitative *in vivo* assessment of the mechanisms for elastic energy storage and return at the ankle joint during human walking. Essentially, the plantar flexor muscles and their long compliant tendon act like a catapult. The Achilles tendon slowly stores elastic energy during most of the stance, releasing it with timing that produces a rapid recoil with very high push-off peak mechanical power output (8,12). The idea that the Achilles tendon could act to amplify mechanical power of the triceps surae muscles (soleus and gastrocnemius) during the push-off phase of walking was proposed by Hof *et al.* (11) more than 25 years ago.

One important feature of the ankle "catapult mechanism" is that the stretch and recoil of the Achilles tendon allows muscle fibers to remain nearly isometric, producing high forces with very little mechanical work (Fig. 2). Muscles spend much less metabolic energy to produce force isometrically when compared with shortening contractions that produce positive mechanical work (23). Thus, the elastic contribution at the ankle joint could save a significant amount of metabolic energy during walking. *In vivo* ultrasound imaging data have revealed the mechanics of the spring in the human walking step, but the metabolic benefits of tendon recoil across the lower limb have proven more difficult to uncover.

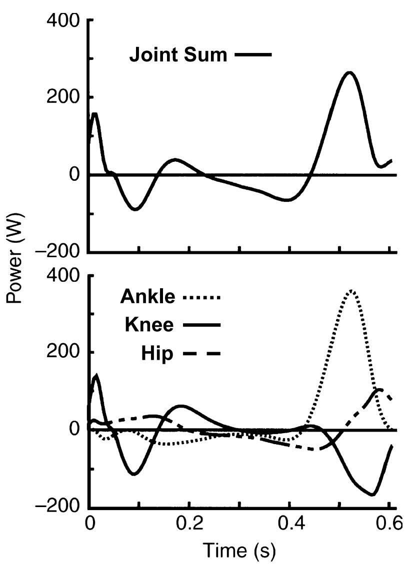

Figure 1. Stance limb mechanical power during walking. Bottom panel shows the instantaneous rate of mechanical energy production (watts) for each of the lower limb joints (ankle, knee, and hip) of a single limb over the stance phase of level walking at 1.52 m·s^{-1}. Positive values indicate energy generation, and negative values indicate energy absorption. Top panel is the sum total power produced by the ankle, knee, and hip. The ankle joint generates a large portion of the positive mechanical power during stance. [Adapted from DeVita P, Helseth J, Hortobagyi T. Muscles do more positive than negative work in human locomotion. *J. Exp. Biol.* 2007; 210:3361–3373. Copyright © 2007 the Company of Biologists Ltd. Used with permission].

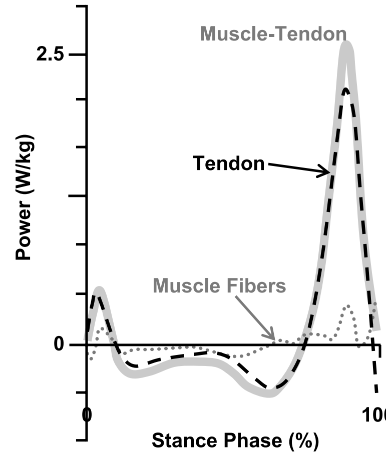

Figure 2. Ankle joint muscle-tendon catapult mechanism during walking. Ultrasound imaging data from humans walking show the instantaneous rate of mechanical energy production (W·kg^{-1}) for gastrocnemius muscle fibers and Achilles tendon separately. The muscle-tendon power (*bold gray*) is the sum of the gastrocnemius muscle power (*dotted gray*) and the Achilles tendon power (*black dashed*). Positive values indicate energy generation, and negative values indicate energy absorption. The muscle fibers contribute very little to total muscle-tendon mechanical power output, but the Achilles tendon stores and returns a significant amount of mechanical energy. [Adapted from Ishikawa M, Komi PV, Grey MJ, *et al.* Muscle-tendon interaction and elastic energy usage in human walking. *J. Appl. Physiol.* 2005; 99:603–608. Copyright © 2005 The American Physiological Society. Used with permission].

Based on the idea that the ankle catapult mechanism leads to significant metabolic energy savings during walking, we propose the central hypothesis that the apparent efficiency of muscle-tendon positive work increases along a proximal to distal gradient (*i.e.*, increases from hip to knee to ankle). This concept is consistent with observed proximodistal differences in muscle-tendon architecture that presumably impact the functional ability of muscle-tendons to effectively store and return elastic energy. A consequence of our central hypothesis is that redistribution of muscle-tendon mechanical work from distal to proximal muscle-tendons (or vice versa) should greatly impact the metabolic cost of walking.

ROBOTIC ANKLE EXOSKELETON STUDIES

We constructed a robotic ankle exoskeleton to assist human walking. It had a carbon fiber and polypropylene shell with an artificial pneumatic muscle (Fig. 3). The exoskeleton used a proportional myoelectric controller so that the wearer's nervous system was in direct control of when and how much assistance was provided by the exoskeleton artificial pneumatic muscles.

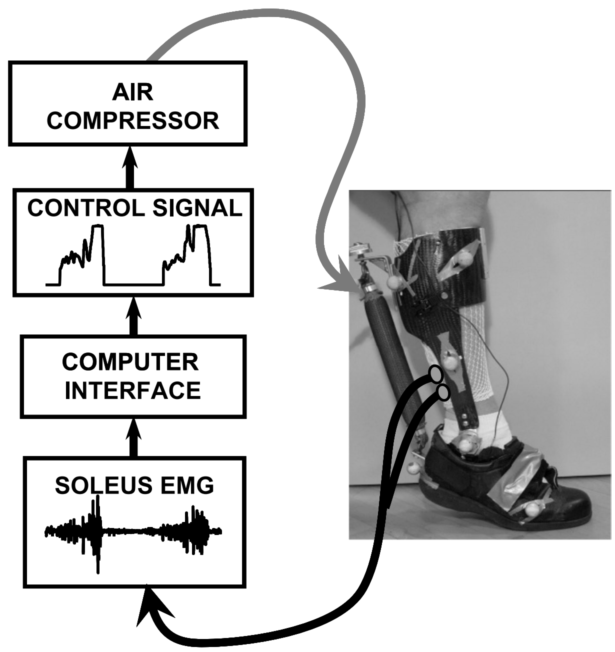

Figure 3. Ankle joint–powered exoskeleton hardware and control. Lightweight carbon fiber ankle-foot orthoses (*i.e.*, exoskeletons) designed to drive ankle plantar flexion with artificial pneumatic muscles during walking. Exoskeletons were controlled using the subject's own soleus surface electromyography (EMG) with proportional myoelectric control. [Adapted from Sawicki GS, Ferris DP. Mechanics and energetics of level walking with powered ankle exoskeletons. *J. Exp. Biol.* 2008; 211: 1402–1413. Copyright © 2008 The Company of Biologists Ltd. Used with permission].

When naive subjects walked with the robotic exoskeleton on one leg, they quickly adapted their muscle activation patterns to substitute exoskeleton work for the combined muscle and tendon work at the ankle joint. Gordon and Ferris (10) found that after two 30-minute training sessions, with the user's soleus muscle providing the control signal, the ankle exoskeleton almost exclusively performed positive mechanical work delivered at push-off. Walking kinematics were nearly identical for powered and unpowered walking. The user's nervous system reduced the triceps surae muscle activity in response to the mechanical assistance, allowing the exoskeleton to replace positive mechanical work that would normally be performed by the biological muscle-tendon unit. Activation of other lower limb muscles showed no differences between unpowered and powered walking conditions (10). This result suggests that the exoskeletons only affected the local muscle-tendon dynamics at the ankle.

Sawicki and Ferris (24–26) examined the effects of using bilateral robotic ankle exoskeletons on the metabolic cost of walking. By measuring oxygen consumption (net metabolic power ($W \cdot kg^{-1}$)) and the mechanical power ($W \cdot kg^{-1}$) produced by the exoskeletons, we could calculate the apparent efficiency of the positive mechanical work at the ankle joint (24). Subjects' metabolic energy expenditure decreased with practice when walking with the robotic ankle exoskeletons. In healthy naive subjects, changes in metabolic cost and exoskeleton mechanics during powered walking reached a steady state after three 30-minute training sessions. At the end of the third session, exoskeletons replaced 22% of the summed lower limb joint (ankle plus knee plus hip) muscle-tendon positive work. In response, subjects reduced their metabolic energy consumption by 10% while walking with exoskeletons powered when compared with walking with exoskeletons unpowered (Fig. 4) (24).

For level walking, we found that the ankle joint apparent efficiency (η^{+}_{ank}) was approximately 0.61 (η^{+}_{ank} = Ankle exoskeleton average positive power ($W \cdot kg^{-1}$)/Δ Net metabolic power ($W \cdot kg^{-1}$)) (24). That is, for every joule of mechanical energy the biological ankle muscle-tendons produced, they consumed approximately 1.6 J of metabolic energy. This efficiency was much higher than would be expected if muscle alone produced all of the ankle muscle-tendon positive work. Reports have found that vertebrate skeletal muscles have an efficiency of positive mechanical work ranging from 0.10 to 0.25. Isolated muscles from rats and mice perform positive mechanical work *in vitro* with an efficiency of 0.10 to 0.19 (28). In whole human studies, the efficiency of walking up a steep slope (where elastic energy storage and return are assumed to be negligible) is approximately 0.25 (19). The ankle joint apparent efficiency we found using our robotic exoskeleton (0.61) was 2.4 to 6 times greater than the numbers suggested by previous studies. These findings strongly suggest that the catapult mechanism substantially enhances the efficiency of ankle muscle-tendon mechanical work and reduces the metabolic energy consumed during walking. Thus, the "spring in your step" has clear energetic benefits.

The apparent efficiency of ankle mechanical work was much lower for walking at fast speeds (Fig. 5) (25) and on uphill inclines (26). Both perturbations greatly increased the amount of positive mechanical work required from the ankle joint muscle-tendons. We found an ankle joint apparent efficiency of 0.38 for a 15-degree incline walking and 0.38 for walking at 1.75 $m \cdot s^{-1}$ (Fig. 5). When increasing walking incline or speed, the lowest efficiency values we measured (0.38) were still greater than those from isolated muscle studies (0.10–0.19). This suggests that even during walking tasks that demand a large mechanical workload from the muscle fibers, the Achilles' tendon still enhances muscle-tendon mechanical efficiency.

NOT ALL MUSCLE-TENDONS ARE CREATED EQUAL

During human walking, the muscle-tendons spanning the major joints of the lower limb can perform different mechanical functions. A muscle-tendon can function as a rigid strut to transfer mechanical energy, as a motor to produce mechanical energy, as a damper to dissipate mechanical energy, or as a spring to store and return elastic energy (7). These different mechanical tasks have different metabolic costs. In general, positive mechanical work requires more metabolic energy than either isometric force production or negative mechanical work (23). Tendon is a passive tissue, and it is typically assumed that it does not use metabolic energy. As a result, the amount of metabolic energy consumed by a muscle-tendon will depend on the dynamic interplay between the muscle and tendon in performing a given mechanical action.

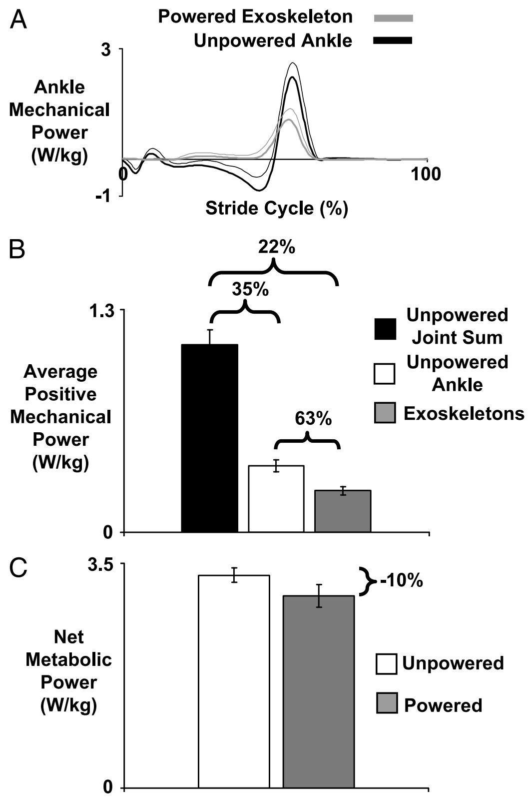

Figure 4. Mechanical power and net metabolic power during powered walking at 1.25 m·s^{-1}. A. The figure shows mean (*thick black*) and 1 SD (*thin black*) mechanical power delivered by the ankle joint over the stride from heel-strike (0%) to ipsilateral heel-strike (100%). The mean contribution of the exoskeleton mechanical power (*thick gray*) +1 SD (*thin gray*) is overlaid. Mechanical power is computed as the product of exoskeleton torque and ankle joint angular velocity and is normalized by subject mass. Positive power indicates energy transferred to the user and negative power indicates energy absorbed from the user. B. The figure shows the mean positive mechanical power delivered by the sum of the ankle, knee, and hip joints (*black*), and ankle joint (*white*) during unpowered walking and the exoskeletons (*gray*) during powered walking. Error bars are SEM. Brackets indicate the percentage contribution comparison between bars (*right to left*). For example, the exoskeleton average positive mechanical power was 63% of the ankle joint average positive mechanical power over the stride. C. The figure shows the mean net metabolic power during unpowered (*white*) and powered (*gray*) walking. Error bars are SE0 Right bracket indicates the change in net metabolic power as a percentage difference from unpowered walking (−10%). Mechanical and metabolic power values are normalized by subject mass. [Adapted from Sawicki GS, Ferris DP. Mechanics and energetics of level walking with powered ankle exoskeletons. *J. Exp. Biol.* 2008; 211:1402–1413. Copyright © 2008 The Company of Biologists Ltd. Used with permission].

Knee muscle-tendons act mainly to absorb energy during walking. During early stance, the knee joint functions as a shock absorber, flexing to cushion weight bearing onto the leading leg. Later, during the push-off phase, the knee joint flexes in preparation for swing but resists the flexion with extensor muscle action. In both cases, the net muscle moment and joint angular velocity are opposite in direction. This results in energy absorption (*i.e.*, negative work) rather than energy production (*i.e.*, positive work). The efficiency of negative muscle work (approximately −1.20) is approximately five times greater than the efficiency of positive muscle work (~0.25) (19). As a result of the relatively high efficiency of negative muscle work, the effect of knee joint musculature on metabolic energy expenditure is probably very low.

In contrast to the knee, muscle-tendons at the hip joint generate mechanical energy (positive work) that far outweighs the energy they absorb (negative work). During early stance, the hip performs positive work as it extends, assisting the trunk as it vaults over the stance limb. Then there is a small amount of negative work at the hip just after midstance, when hip extension transitions to hip flexion. During the push-off phase of late stance, a large burst of positive work is performed at the hip to help accelerate the swing leg. Given the large amount of positive work performed by hip joint muscle-tendons during human walking, and the low efficiency (~0.25) for positive muscle work, it is logical to conclude that a large fraction of the metabolic energy is consumed by hip muscle-tendons during walking. This conclusion must be drawn with caution because mechanical work need not be performed only by active muscles with a metabolic cost. Passive elastic tissues can also perform both positive and negative work with little metabolic cost.

The link between the mechanical function of a muscle-tendon and the metabolic energy it consumes is largely determined by its architecture (3,22). For example, the plantar flexors have relatively short muscle fibers (<5 cm) in a pennation arrangement (5–30 degrees) and large physiological cross-sectional areas (30). In addition, the plantar flexors have a long compliant series tendon (*i.e.*, the Achilles). Short fibers and a long tendon combine to give high fixed-end compliance (22), a characteristic that is particularly suited for elastic energy storage and return and economical force production (3). In contrast, although hip flexor and extensor muscles have large cross-sectional areas like the plantar flexors, they have much longer fibers (>6 cm) and much smaller pennation angles (~5 degrees) (30). A more critical factor is that hip muscles do not possess long compliant series tendons and as a consequence have relatively low fixed-end compliance. Low fixed-end compliance is suited for performing muscle fiber work rather than force under isometric conditions. The muscle fiber work likely comes at a substantial metabolic cost (3). Although the ankle and hip muscle-tendons both act to perform substantial positive work during walking, key differences in their muscle-tendon architecture may influence the amount of metabolic energy they consume.

These specific differences in ankle and hip musculature in humans have been more generally described using the concept of a proximodistal gradient for muscle-tendon architecture in legged animals (4). Proximal muscle-tendons in the legs tend to have long muscle fibers and relatively short free tendons. Distal muscles in the legs tend to have shorter muscle fibers with high pennation angles and long elastic tendons. As a result, larger proximal muscles are more likely to be sources of high muscular work output (and metabolic energy consumption), whereas distal muscles, because of their long series tendons can produce force nearly isometrically, consuming smaller amounts of metabolic energy.

These observations support our central hypothesis that differences in architecture (*e.g.*, fixed-end compliance) of

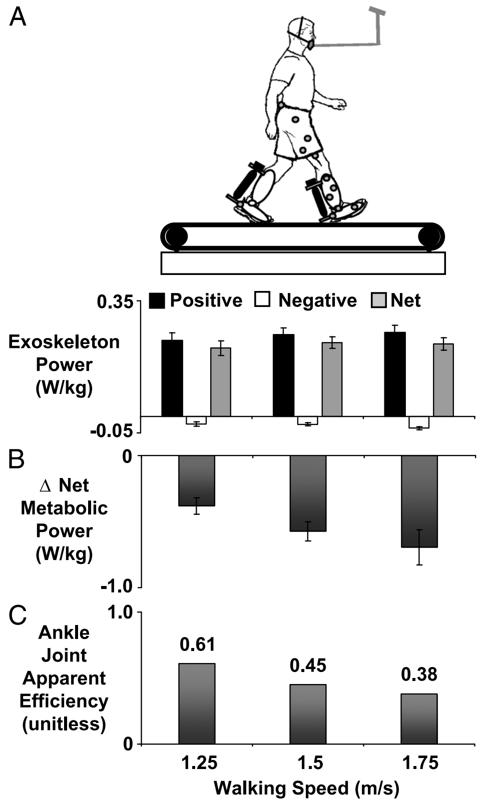

Figure 5. Exoskeleton mechanical power, net metabolic power, and ankle joint apparent efficiency with increasing walking speed. Bars indicate nine subjects mean (A) exoskeleton average positive (*black*), negative (*white*), and net (*gray*) mechanical power over a stride for powered walking, (B) change in net metabolic power (powered-unpowered) caused by powered assistance from bilateral ankle exoskeletons, and (C) ankle joint apparent efficiency. Apparent efficiency is computed as the ratio of average exoskeleton positive mechanical power to the resulting reduction in net metabolic power and assumes that artificial muscle work directly replaces biological muscle work. For all panels, walking speed increases from left (1.25 m·s^{-1}) to right (1.75 m·s^{-1}). All metabolic power values are normalized by subject mass. Error bars are SEM. [Adapted from Sawicki GS, Ferris DP. Mechanics and energetics of level walking with powered ankle exoskeletons. *J. Exp. Biol.* 2008; 211:1402–1413. Copyright © 2008 The Company of Biologists Ltd. Used with permission].

the muscle-tendons spanning the hip, knee, and ankle joints yield a proximal to distal gradient in the efficiency of muscle-tendon positive work. That is, the highest muscle-tendon efficiencies occur at the more compliant distal joints.

ESTIMATES OF METABOLIC COST OF ANKLE, KNEE, AND HIP WORK

Using a simple relationship between metabolic and mechanical energy expenditure and our measurements from exoskeleton walking, it is possible to estimate independent contributions of the muscle-tendons at each of the lower limb joints to the overall metabolic energy expenditure of walking (Fig. 6).

The efficiency (η) of mechanical work can be defined as the ratio of mechanical energy output to the metabolic energy input required to perform the work. Following this definition, and acknowledging that positive and negative work are performed with different efficiencies, we can write a general expression for the net metabolic power of walking (net refers to the metabolic power above that required for upright quiet standing) (equation 1):

$$P_{\text{net met}} = \frac{\overline{P^{+}}_{\text{mech } \Sigma \text{ joints}}}{\eta^{+}_{\Sigma \text{ joints}}} + \frac{\overline{P^{-}}_{\text{mech } \Sigma \text{ joints}}}{\eta^{-}_{\Sigma \text{ joints}}} \qquad [1]$$

Equation 1 indicates that the net metabolic power (($P_{\text{net met}}$) *i.e.*, the rate of metabolic energy consumption) equals the sum of the metabolic costs to perform both positive work and negative work across the lower limb joints. The contributions of mechanical work to metabolic cost are given as the average (indicated by horizontal bars) mechanical power of the three joints ($\boldsymbol{\Sigma}_{\text{joints}}$ = ankle average + knee average + hip average) for both legs over a stride divided by the efficiency of mechanical work (η^{+} for positive work; η^{-} for negative work).

In our calculations, we assumed that the metabolic cost of negative work is negligible during walking. This assumption is reasonable given that 1) the lower limb muscles perform approximately 50% to 300% more positive than negative work during walking (6,29), 2) the efficiency of negative muscle work (−1.20) is much higher than the efficiency of positive muscle work (0.10–0.25) (19), and 3) tendons and ligaments likely perform some of the negative work (with very little metabolic cost) during walking rather than being entirely performed by muscles. Furthermore, based on data for summed joint positive (1.44 W·kg^{-1}) and negative (0.74 W·kg^{-1}) power (29), and using η^{+} = 0.25 and η^{-} = −1.20, we estimated that positive work accounts for 90% of the total metabolic cost of walking, whereas negative work only accounts for 10% of the total metabolic cost of walking. Given this result, we simplified our analysis by eliminating the negative work term in equation 1.

We made a second assumption that the metabolic cost of walking can be separated into independent contributions from the ankle, knee, and hip muscle-tendons, each generating positive mechanical work with different efficiencies (equation 2). This assumption is based on the premise that differences in muscle-tendon architecture can alter the relationship between mechanical and metabolic energy expenditure (discussed in previous section Not All Muscle-Tendons Are Created Equal):

$$P_{\text{net met}} = \frac{\overline{P^{+}}_{\text{mech ankle}}}{\eta^{+}_{\text{ankle}}} + \frac{\overline{P^{+}}_{\text{mech knee}}}{\eta^{+}_{\text{knee}}} + \frac{\overline{P^{+}}_{\text{mech hip}}}{\eta^{+}_{\text{hip}}} \qquad [2]$$

Our data from nine subjects (mean mass, 77.8 kg) walking at 1.25 m·s^{-1} (mean stride period, 1.17 seconds) with unpowered ankle exoskeletons indicated a net metabolic power of 3.39 W·kg^{-1} (3.39 W·kg^{-1} × 77.8 kg × 1.17 s = 308 J) (24). Inverse dynamics calculations during unpowered exoskeleton walking yielded average positive mechanical power for ankle (0.38 W·kg^{-1} = 35 J), knee (0.20 W·kg^{-1} = 18 J), and hip (0.47 W·kg^{-1} = 43 J). By comparing unpowered and powered walking mechanics and energetics, we computed an apparent efficiency of ankle joint positive work of 0.61. With these data, we estimated the apparent efficiency for positive

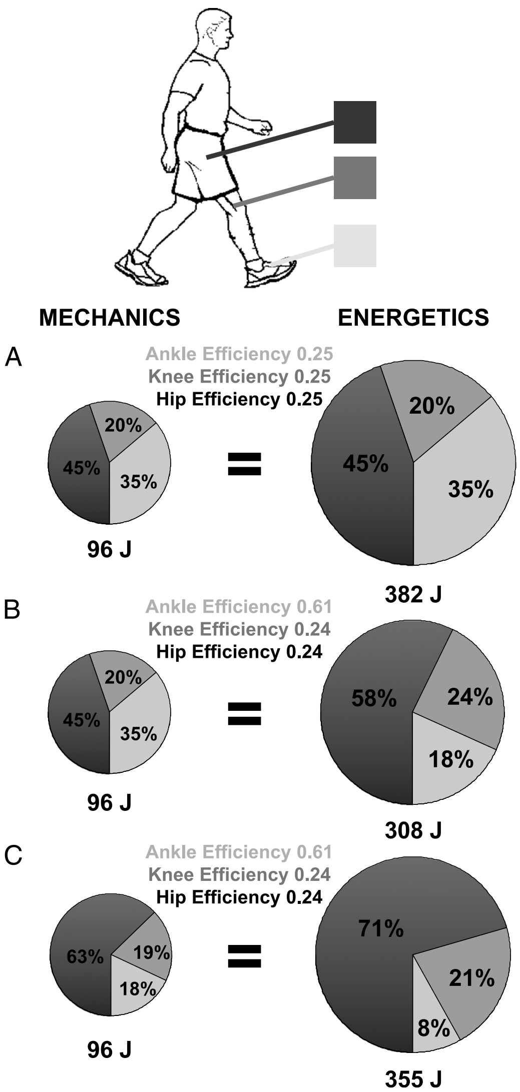

Figure 6. Schematic of joint muscle-tendon level mechanics and energetics of human walking. Pie charts indicate the relative amounts (%) of ankle (*light gray*), knee (*medium gray*), and hip (*dark gray*) positive mechanical work (*left column*) and metabolic energy (*right column*). The area of each pie chart reflects the magnitude of the total energy per stride that is also displayed numerically below each pie chart. The apparent efficiencies used to convert mechanical energy values to metabolic energy values are indicated in the center column. In panel A, we assumed that all the joints performed positive mechanical work with identical efficiencies set at 0.25 (19). This results in an overestimate of the measured metabolic cost. In panel B, we set the efficiencies so that the ankle joint efficiency matches our measured value of 0.61 (24). The knee and hip were assumed to operate with equal efficiencies (0.24) such that the metabolic energy matched the measured total net metabolic cost per stride (308 J). In panel C, we computed values for a compensated gait, where half of the ankle joint work was redistributed to the hip joint. This is meant to represent a hypothetical individual with reduced ankle plantar flexor power at push-off (*e.g.,* amputee, stroke, or spinal cord injury). Reducing ankle plantar flexor work by 50% and compensating with extra hip work results in a 15% increase in metabolic cost.

mechanical work at the knee and hip joints during human walking (assuming they are equal for the sake of simplicity). This was done by combining the second and third terms on the right hand side of equation 2 and solving for the combined knee/hip apparent efficiency (equation 3). Solving equation 3 yielded a knee/hip apparent efficiency of 0.24:

$$\eta^{+}{}_{\text{knee/hip}} = \frac{\overline{P^{+}}_{\text{mech knee/hip}}}{\left(P_{\text{net met}} - \dfrac{\overline{P^{+}}_{\text{mech ankle}}}{\eta^{+}{}_{\text{ankle}}}\right)} \qquad [3]$$

It was then possible to estimate the relative contributions (%) of each of the joints to the total metabolic cost (308 J per stride) based on their relative contributions (%) to the summed joint mechanical work (96 J) (Fig. 6B).

Figure 6A shows the metabolic cost of positive work at each of the three joints assuming they all operate with efficiency of 0.25. Using a high-end estimate for muscle efficiency of 0.25 (19) with our measured values of mechanical work resulted in a calculated metabolic cost of 382 J per stride. This overestimated the actual measured metabolic cost (308 J per stride) by 24%. There are two possibilities for this discrepancy: 1) the ankle, knee, and hip muscle-tendons all operate with a higher efficiency of 0.31 or 2) the muscle-tendons at each joint perform positive work with different mechanical efficiencies. Our direct measurement of ankle muscle-tendon efficiency of 0.61 and our back-calculation for knee and hip efficiencies of 0.24 (reasonably close to what would be expected for muscles operating with little or no tendon) support the second possibility.

CLINICAL IMPLICATIONS

Several clinical populations have increased metabolic cost of walking. For some of these populations, a likely contributor to their high energetic cost of locomotion is an inability to exploit the spring in their step. This could be caused by uncoordinated activation of plantar flexor muscles (*e.g.*, individuals with stroke, spinal cord injury, or cerebral palsy), plantar flexor weakness (*e.g.*, older adults), small joint excursions that could limit tendon stretch (*e.g.*, clinical or older populations), or simply the absence of muscles and tendons to effectively store and release elastic energy (*e.g.*, amputees).

A great deal of research has focused on the importance of reflex activation in recruiting the plantar flexor muscles during human locomotion. Evidence suggests that Ia, Ib, and II afferents all play a role in scaling muscle activation appropriately to effectively store and release elastic energy in the Achilles tendon with the right timing (13). Individuals with affected reflex pathways because of neurological conditions may lose the ability to appropriately time their muscle activity to make effective use of elastic energy storage and return during walking. In this case, individuals may redistribute the mechanical workload from ankle muscle-tendons to less efficient muscle-tendons spanning more proximal joints such as the hip and/or knee.

Increased reliance on hip and knee musculature, however, comes at a higher metabolic cost. In Figure 6C, we show how redistributing half of the normal ankle joint muscle-tendon work to the hip might impact metabolic energy consumption. Specifically, there would be an increase in metabolic

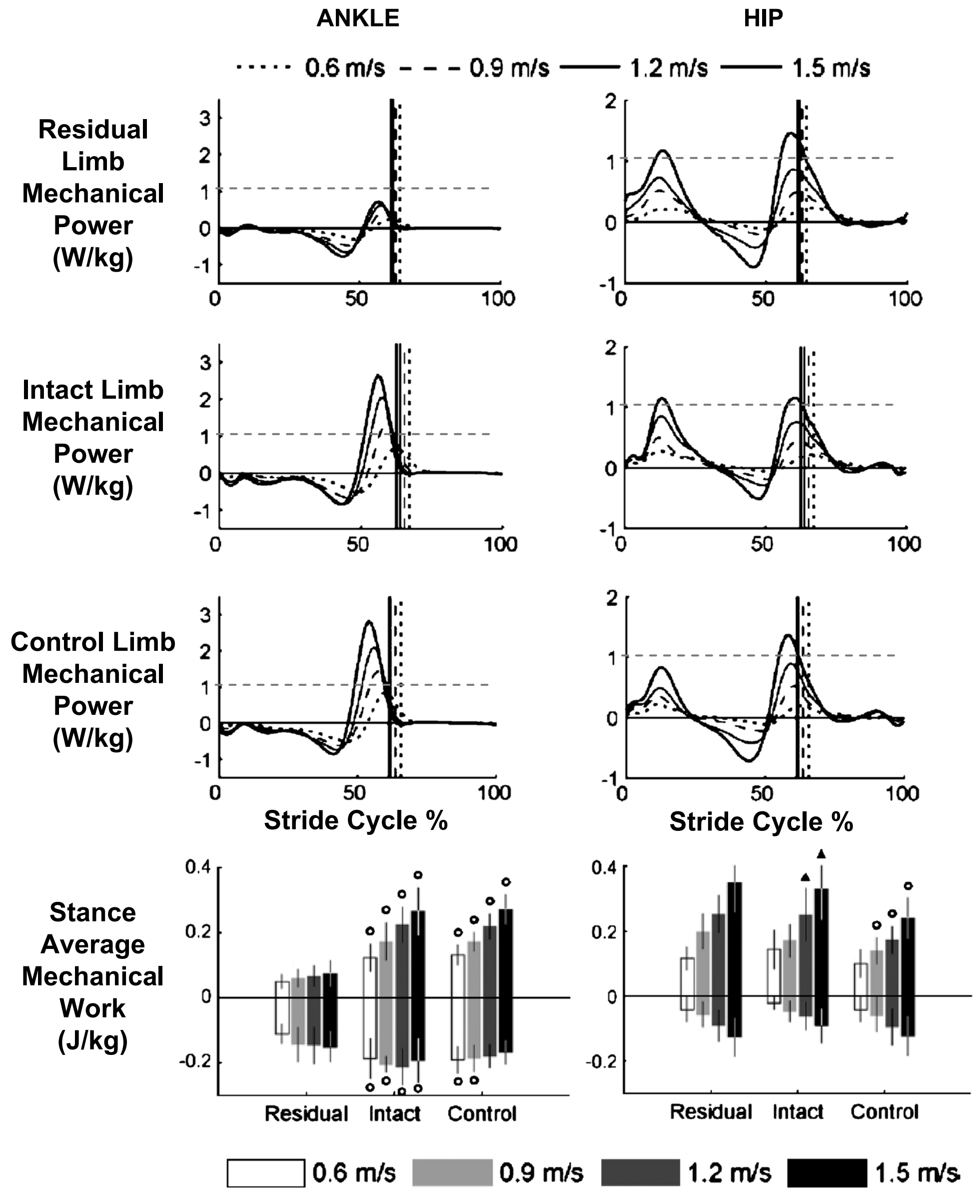

Figure 7. Joint mechanics at the hip and ankle during walking in transtibial amputees. Transtibial amputees walked overground at four speeds (0.6–1.5 $m{\cdot}s^{-1}$) with their own prosthetic feet. Healthy controls followed the same protocol. Graphs show the ankle (*left column*) and hip (*right column*) mechanical power ($W{\cdot}kg^{-1}$; *top three rows*) over the stride cycle (heel strike (0%) to heel strike (100%)) and mechanical work ($J{\cdot}kg^{-1}$; *bottom row bar graphs*) during stance phase for amputee residual, amputee intact and healthy control limbs. In bar graphs, *open circles* indicate a statistically significant difference with the residual limb and *dark triangles* a statistically significant difference between intact and control limbs. For amputees, the power generated by the prosthetic ankle at push-off (~60% of stride) is markedly reduced compared with the intact ankle and the healthy control ankle. Conversely, hip power generation is markedly increased for the amputee limbs when compared with controls, demonstrating a redistribution from ankle power to hip power. [Adapted from Silverman AK, Fey NP, Portillo A, *et al.* Compensatory mechanisms in below-knee amputee gait in response to increasing steady-state walking speeds. *Gait Posture* 2008; 28:602–609. Copyright © 2008 Elsevier. Used with permission].

energy consumption of approximately 15% compared with the metabolic energy consumption during walking with the normal distribution of lower-limb joint muscle-tendon work.

Transtibial amputees are a particularly interesting example of this redistribution of work. On the side of the amputation, there is no Achilles tendon to store and return elastic energy. Elastic prosthetic limbs attempt to provide energy storage and return during walking but produce little to no metabolic savings for the user (17). This limited benefit may be because a relatively small fraction of the strain energy stored in the elastic prosthesis is recovered (~40%) (21) compared with the Achilles tendon, which, like most biological tendons, returns 80% to 90% (*i.e.*, 10%–20% hysteresis) of the energy stored when it is stretched. Furthermore, unlike the catapult mechanism of the Achilles tendon, which can store energy throughout stance and focus the release at push-off, only a small portion of the energy stored in many elastic prostheses is returned at the appropriate time (17,21).

Because of deficits in ankle push-off mechanical power, transtibial amputees must rely on more proximal muscle-tendons to provide the needed mechanical energy to power their gait (27). The loss of active ankle plantar flexion at

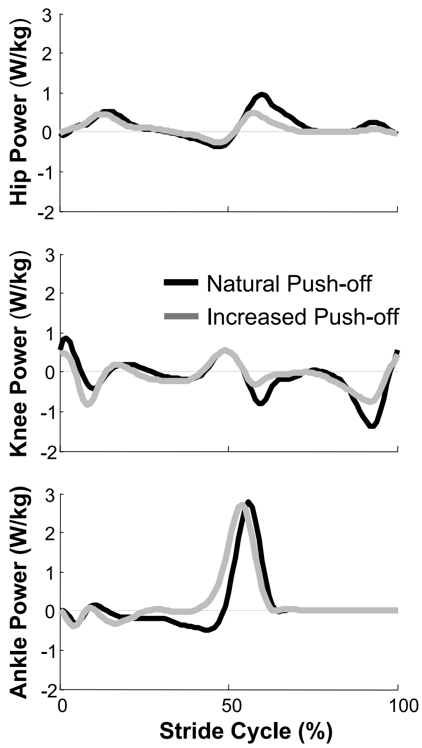

Figure 8. Joint mechanical powers at the hip, knee, and ankle during gait with natural and increased push-off. Healthy subjects walked at 1.25 m·s^{-1} with natural gait (*black*) and consciously increasing plantar flexion push-off (*gray*). The shift between ankle and hip joint powers is apparent as hip power generation at the end of stance is lower in the increased push-off condition compared with natural push-off. [Adapted from Lewis CL, Ferris DP. Walking with increased ankle push-off decreases hip muscle moments. *J. Biomech* 2008; 41:2082–2089. Copyright © 2008 Elsevier. Used with permission].

push-off is readily apparent when comparing the mechanical power produced by the amputee residual limb to a healthy control limb during walking (Fig. 7). Healthy subjects generate peak ankle power of approximately 2 W·kg^{-1} (at 1.2 m·s^{-1}), whereas amputees generate only approximately 0.5 W·kg^{-1} in their residual limb (27). Amputees compensate for lack of ankle push-off power by increasing hip power early in stance in both the residual and intact limbs. For example, although residual ankle muscle-tendon mechanical work is significantly lower during stance in amputees (~0.06 J·kg^{-1}) when compared with healthy controls (~0.22 J·kg^{-1}), hip muscle-tendon mechanical work is significantly higher in amputees (in both the residual and intact limbs, ~0.25 J·kg^{-1}) when compared with healthy controls ((0.18 J·kg^{-1}) Fig. 7 bottom panel) (27). This abnormal distribution (or redistribution) of mechanical power to the hip may help explain the high metabolic cost of walking in amputees, even while using an energy-storing prosthetic foot (*e.g.*, Fig. 6C).

Redistribution of mechanical energy within the lower limb during walking may be bidirectional. That is, in addition to the possibility that ankle muscle-tendon work can be compensated for by the hip (*e.g.*, as in amputees), mechanical work normally performed by the hip muscle-tendons might be accomplished at the knee or ankle. For example, when Lewis and Ferris instructed healthy subjects to simply "push more with your foot" when they walked, they found a significant reduction in peak moment, power, and angular impulse for hip flexion, as well as lower peak moment and angular impulse for hip extension (18). These changes accompanied increased plantar flexor work at push-off (Fig. 8) (18). These findings, along with the observed redistribution of mechanical work within the amputee lower limb, indicate a clear trade-off between ankle and hip mechanical power during human walking. Future research should continue to test the generality of this hip-ankle powering trade-off, the neural mechanisms involved, and its potential influence on the metabolic energy expenditure during human walking.

SUMMARY

Because of a variety of factors, particularly differences in muscle-tendon architecture, we argue that the muscle-tendons of the lower limb perform mechanical work during human walking with efficiency that increases from proximal to distal joints. Plantar flexors at the ankle use the Achilles tendon to store and return elastic energy and achieve an especially high efficiency of approximately 0.61 during level walking at intermediate speeds. We estimate that muscle-tendons at the knee and hip, with their shorter tendons and smaller pennation angles, perform positive mechanical work with much lower efficiency (~0.24). Evidence points toward an inherent trade-off in power production between the hip and ankle such that deficiencies or excesses at one joint are compensated for by the other joint. Because of differences in lower limb joint muscle-tendon efficiencies, reliance on hip work to compensate for decreased ankle work could substantially increase the metabolic cost of locomotion. Thus, the high metabolic cost of walking in a number of populations such as neurologically impaired individuals, the elderly, and amputees may all be partially explained by a redistribution of mechanical work away from relatively efficient distal (*e.g.*, ankle) muscle-tendons to comparatively inefficient proximal (*e.g.*, hip) muscle-tendons.

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