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Powered ankle exoskeletons reveal the metabolic cost of plantar flexor mechanical work during walking with longer steps at constant step frequency

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SUMMARY

We examined the metabolic cost of plantar flexor muscle–tendon mechanical work during human walking. Nine healthy subjects walked at constant step frequency on a motorized treadmill at speeds corresponding to 80% (1.00 $m\,s^{-1}$), 100% (1.25 $m\,s^{-1}$), 120% (1.50 $m\,s^{-1}$) and 140% (1.75 $m\,s^{-1}$) of their preferred step length (L*) at 1.25 $m\,s^{-1}$. In each condition subjects donned robotic ankle exoskeletons on both legs. The exoskeletons were powered by artificial pneumatic muscles and controlled using soleus electromyography (i.e. proportional myoelectric control). We measured subjects' metabolic energy expenditure and exoskeleton mechanics during both unpowered and powered walking to test the hypothesis that ankle plantarflexion requires more net metabolic power ($W\,kg^{-1}$) at longer step lengths for a constant step frequency (i.e. preferred at 1.25 $m\,s^{-1}$). As step length increased from 0.8 L* to 1.4 L*, exoskeletons delivered ~25% more average positive mechanical power (P=0.01; +0.20±0.02 $W\,kg^{-1}$ to +0.25±0.02 $W\,kg^{-1}$, respectively). The exoskeletons reduced net metabolic power by more at longer step lengths (P=0.002; –0.21±0.06 $W\,kg^{-1}$ at 0.8 L* and –0.70±0.12 $W\,kg^{-1}$ at 1.4 L*). For every 1 J of exoskeleton positive mechanical work subjects saved 0.72 J of metabolic energy ('apparent efficiency'=1.39) at 0.8 L* and 2.6 J of metabolic energy ('apparent efficiency'=0.38) at 1.4 L*. Declining ankle muscle–tendon 'apparent efficiency' suggests an increase in ankle plantar flexor muscle work relative to Achilles' tendon elastic energy recoil during walking with longer steps. However, previously stored elastic energy in Achilles' tendon still probably contributes up to 34% of ankle muscle–tendon positive work even at the longest step lengths we tested. Across the range of step lengths we studied, the human ankle muscle–tendon system performed 34–40% of the total lower-limb positive mechanical work but accounted for only 7–26% of the net metabolic cost of walking.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/212/1/21/DC1

Key words: locomotion, walking, step length, metabolic cost, exoskeleton, ankle, human, inverse dynamics, joint power, efficiency.

INTRODUCTION

During human walking, a substantial amount of mechanical work is performed on the center of mass during the step-to-step transition (Kuo et al., 2005). Donelan et al. used force platforms under each limb (i.e. individual limbs method) to demonstrate that during double support, the leading leg performs negative work to redirect the center of mass while the trailing leg performs positive work to restore lost energy (Donelan et al., 2002a; Donelan et al., 2002b). The trailing leg impulse begins just prior to the leading leg heel-strike (i.e. a pre-emptive push-off occurs), reducing the leading leg collision and the magnitude of positive work required to redirect the center of mass velocity (Donelan et al., 2002a; Kuo, 2002; Ruina et al., 2005).

Although a pre-emptive push-off can help reduce collision losses, the trailing leg still must perform positive mechanical work during double support. Trailing limb positive mechanical work constitutes ~60–70% of the total positive work performed over a stride and the ankle plantar flexors provide the majority of that work (Kuo et al., 2005). Theoretical analyses of simple bipedal walking models (Kuo, 2002; Ruina et al., 2005) and empirical measurements on humans (Donelan et al., 2002a; Donelan et al., 2002b) both indicate that step-to-step transition positive mechanical work increases with step length to the fourth power. Net metabolic power during human walking also increases in proportion to the fourth power of step length (Donelan et al., 2002a). These data indicate that the step-to-step transition probably accounts for ~60–70% of the total net metabolic power ($W\,kg^{-1}$) during walking (Donelan et al., 2002a; Kuo et al., 2005).

Although we know that plantar flexor muscle–tendons generate the largest power burst during trailing limb push-off (Eng and Winter, 1995; Gitter et al., 1991; Meinders et al., 1998), inverse dynamics cannot separate positive work performed by plantar flexor muscles from positive work delivered by previously stored elastic energy in the Achilles' tendon. Recent studies using ultrasound have directly examined *in vivo* muscle–tendon behavior in walking humans. Results indicate that the Achilles' tendon stores energy throughout stance and then recoils rapidly contributing significantly to trailing limb ankle muscle–tendon mechanical power output during the push-off phase of the step-to-step transition (Fukunaga et al., 2001; Ishikawa et al., 2005; Ishikawa et al., 2006; Lichtwark et al., 2007; Lichtwark and Wilson, 2006; Lichtwark and Wilson, 2007). Ultrasound studies have not yet examined the effects of increasing walking speed on plantar flexor–Achilles' muscle–tendon mechanics and energetics. Indirect evidence, suggests that the contribution of the Achilles' tendon to ankle muscle–tendon positive power may be highly speed dependent (Hansen et al., 2004; Hof et al., 2002; Neptune et al., 2008).

In a previous study, we showed that bilateral robotic lower-limb exoskeletons can be used to examine the metabolic cost of ankle muscle–tendon mechanical work during human walking (Sawicki and Ferris, 2008). We assumed that exoskeleton artificial pneumatic muscles directly replaced plantar flexor muscle–tendon positive mechanical work. Reported values of the 'muscular efficiency' (η^{+}_{muscle}) of positive work for mammalian skeletal muscle range from 0.10–0.34, with many sources assuming an average of ~0.25 (Gaesser and Brooks, 1975; Margaria, 1968; Ryschon et al., 1997; Smith et al., 2005; Whipp and Wasserman, 1969). Comparison of changes in net metabolic power and average mechanical power at the ankle joint in our previous exoskeleton study yielded an 'apparent efficiency' of ankle muscle–tendon positive mechanical work of 0.61 for walking at $1.25\,m\,s^{-1}$. Our results were indicative of the Achilles' tendon performing ~59% of the plantar flexor muscle–tendon positive work (assuming η^{+}_{muscle}=0.25) (Sawicki and Ferris, 2008). We estimated that the plantar flexor muscle–tendons performed ~35% of the total lower limb positive mechanical work, but consumed only ~19% of the total metabolic energy during level walking at $1.25\,m\,s^{-1}$.

The purpose of the present study was to extend our previous exoskeleton results to examine the metabolic cost of plantar flexor muscle–tendon work at longer step lengths. Humans normally increase walking speed by increasing both step length and step frequency. However, step-to-step transition mechanical and metabolic energy expenditure depends most strongly on step length (~step length^4) (Donelan et al., 2002a; Donelan et al., 2002b). We chose to have our subjects increase walking speed by increasing step length only (i.e. while holding step frequency constant). This kept frequency-dependent metabolic costs (e.g. leg swing) constant and resulted in larger increases in step-to-step transition mechanical and metabolic power requirements than would be expected for natural increases in speed (see Materials and methods for more details). We hypothesized that the 'apparent efficiency' of plantar flexor muscle–tendon positive work would decrease at longer step lengths. We based this hypothesis on the expectation that as speed and step length increased, the plantar flexor muscle fibers would deliver a larger fraction of the ankle muscle–tendon positive work than elastic energy from the recoiling Achilles' tendon. An inherent assumption of this study was that the exoskeleton mechanical work would replace ankle muscle–tendon mechanical work rather than augment it. As such, we expected triceps surae muscle activation to be less during walking with the powered exoskeletons compared to walking without exoskeleton assistance for all speed–step length conditions. To test these predictions, we compared subjects' net metabolic power and electromyography amplitudes with ankle exoskeletons powered *versus* unpowered during level, steady-speed walking at various step lengths and a constant step frequency (i.e. preferred at $1.25\,m\,s^{-1}$).

MATERIALS AND METHODS

Subjects

We recruited nine (5 males, 4 females) healthy subjects (body mass=80.3±14.7 kg; height=179±3 cm; leg length=92±2 cm) to participate in the study. Each subject had at least 90 min (three or more 30-min practice sessions) of previous practice walking with powered exoskeletons and exhibited no gait abnormalities. In accordance with the Declaration of Helsinki, subjects read and signed a consent form approved by the University of Michigan Institutional Review Board for Human Subject research before testing.

Exoskeletons

We custom built lightweight [mass=1.18±0.11 kg each (mean ± s.d.)] bilateral, ankle-foot exoskeletons (i.e. orthoses) for each subject. The exoskeletons allowed free rotation about the ankle plantar/dorsiflexion axis. We used a metal hinge joint to connect a carbon fiber shank to a polypropylene foot section. We used two stainless steel brackets to attach a single artificial pneumatic muscle (length=45.6±2.2 cm; moment arm=10.6±0.9 cm) along the posterior shank of each exoskeleton. We used a physiologically inspired controller to command the exoskeleton plantar flexor torque assistance with timing and amplitude derived from the user's own soleus electromyography (i.e. proportional myoelectric control) (Gordon and Ferris, 2007; Sawicki and Ferris, 2008). Specific details on the design and performance of the exoskeletons are documented elsewhere (Ferris et al., 2005; Ferris et al., 2006; Gordon et al., 2006; Sawicki and Ferris, 2008; Sawicki et al., 2005).

Protocol

Experienced (>90 min walking with powered exoskeletons) subjects walked on a motorized treadmill with bilateral ankle exoskeletons unpowered then powered at four different speeds/step lengths [0.8×, 1.0×, 1.2× and 1.4× preferred step length (L*) for unpowered walking at $1.25\,m\,s^{-1}$] (Donelan et al., 2002a; Donelan et al., 2002b) (Fig. 1; supplementary material Movie 1). Our previous research demonstrated no further reductions in net metabolic power ($W\,kg^{-1}$) after 90 min of powered walking practice (Sawicki and Ferris, 2008). We determined subjects' preferred step period (seconds) using a stopwatch to record the mean time of three 100-step intervals during unpowered treadmill walking at $1.25\,m\,s^{-1}$. We took the reciprocal of the mean step period to get the preferred step frequency ($steps\,s^{-1}$) at $1.25\,m\,s^{-1}$. Then we divided the treadmill belt speed ($m\,s^{-1}$) by the step frequency ($steps\,s^{-1}$) to get the preferred step length ($m\,step^{-1}$) at $1.25\,m\,s^{-1}$ (1.0 L*). We used a metronome to enforce subjects' preferred step frequency at $1.25\,ms^{-1}$ for all conditions. We adjusted the treadmill belt speed to constrain subjects' step lengths. The 0.8 L*, 1.0 L*, 1.2 L* and 1.4 L*, step-length conditions corresponded to ~1.00, 1.25, 1.50 and $1.75\,m\,s^{-1}$ treadmill belt speeds, respectively. We could have studied the step-to-step transition allowing subjects to increase walking speed naturally by choosing their preferred step length and step frequency. Instead, we chose to constrain step frequency and vary step length, for two reasons. First, this protocol allowed us to enforce step-to-step transition center of mass mechanical and net metabolic power to follow a known strong proportional relationship with the step length (~step length^4) (Donelan et al., 2002a; Donelan et al., 2002b) in all walking conditions. This helped limit potential confounding effects of frequency-dependent changes in metabolic cost between powered and unpowered walking conditions (e.g. swing leg costs). Some estimates of swing leg metabolic cost are as high as 33% of the total metabolic cost (Doke et al., 2005). Second, manipulating step length at a fixed step frequency in order to alter speed increased the range of mechanical and net metabolic power requirements considerably beyond what could be studied if subjects chose their preferred step frequency at each speed. We estimate the percentage difference in step lengths we studied compared to preferred step lengths are –12%, 0%, +14%, and +19% for 1.0, 1.25, 1.5 and $1.75\,m\,s^{-1}$, respectively.

Step-length conditions were presented in random order, but for each step length we followed the same walking timeframe (Fig. 1). First subjects walked for 7 min with exoskeletons unpowered (unpowered). Then subjects rested for 3 min. Finally, subjects walked for 7 min with exoskeletons powered (powered). If the peak force output of the artificial muscles (and exoskeleton torque) is similar in each step-length condition, then observed differences in average exoskeleton mechanical power output across conditions would be attributed to changes in ankle joint kinematics (range of motion, ankle joint angular velocity) rather than changes in artificial muscle force output. Thus, we tuned the proportional

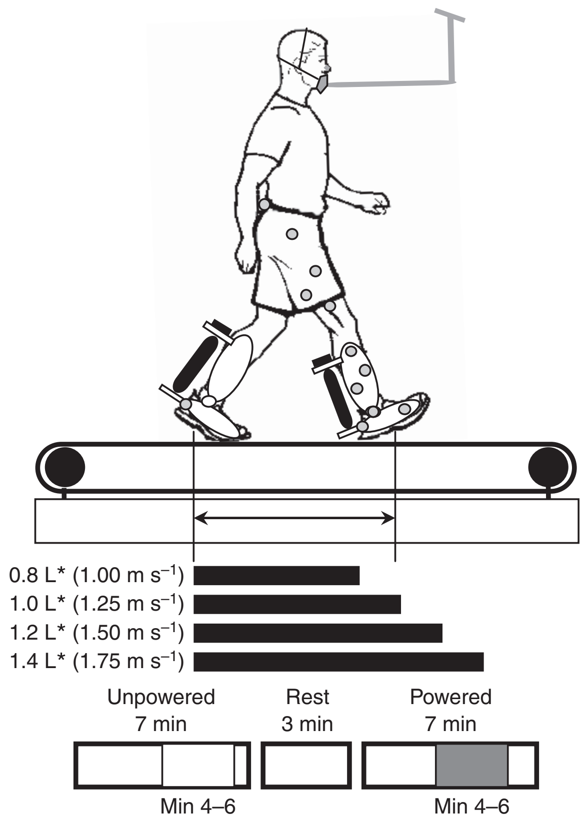

Fig. 1. Experimental set-up. Subjects walked on a motorized treadmill for 7 min with exoskeletons unpowered, then rested for 3 min, then walked for 7 min with exoskeletons powered, while a metronome enforced their preferred step frequency (from unpowered walking at 1.25 m s^{-1}). Treadmill belt speed was set to achieve speed/step-length conditions of 0.8, 1.0, 1.2 and 1.4× the preferred step length at 1.25 m s^{-1} (L*; i.e. 1.00, 1.25, 1.50 and 1.75 m s^{-1}). Conditions were presented in randomized order. The boxes indicate periods when data were collected (minutes 4–6) in both unpowered and powered conditions. We collected joint kinematics using motion capture and reflective markers, O_2 consumption and CO_2 production using a metabolic cart, ankle muscle activation patterns using surface electromyography and artificial muscle forces using series load transducers.

myoelectric controller during the unpowered walking bout for each step length separately. We set the gain and threshold on soleus surface electromyography so the control signal saturated for at least five consecutive steps. We then doubled the gain in order to encourage reduction in soleus muscle recruitment (Gordon and Ferris, 2007).

Data collection and analysis

We recorded subjects' ankle, knee and hip joint kinematics, whole-body gait kinematics, ankle dorsiflexor and plantar flexor electromyography, and exoskeleton artificial muscle forces. For kinematic, electromyographic and artificial muscle force data we acquired 10 s trials (i.e. ~7–9 walking strides) at the beginning of minutes 4, 5 and 6 during each of the eight (unpowered mode and powered mode for each of four speeds/step lengths) 7 min trials. We measured O_2 consumption and CO_2 production during a single 7 min quiet standing trial of metabolic data for each subject before walking trials commenced. Metabolic data were collected continuously during each of the 7 min speed/step-length conditions.

In addition, on a separate day of testing, we recorded metabolic data while subjects completed each of the speed/step-length conditions on the treadmill without (without) wearing powered exoskeletons. In the same session, we also recorded simultaneous joint kinematics and ground reaction force data for overground walking with unpowered exoskeletons (seven trials for each speed/step-length condition).

Specific details on procedures for analysis of the metabolic cost, kinematics, joint mechanics, exoskeleton mechanics and electromyography data are identical to those in our previous research (Sawicki and Ferris, 2008).

Ankle joint muscle–tendon 'apparent efficiency' *via* exoskeleton performance index

By combining measures of mechanical and metabolic power (W kg^{-1}), we computed the exoskeleton performance index and ankle joint muscle–tendon 'apparent efficiency' ($\eta^{+}_{\mathrm{ankle}}$). First, we subtracted the net metabolic power during unpowered walking from the net metabolic power during powered walking for each speed/step length to obtain the metabolic power savings resulting from the exoskeleton assistance. Muscles perform positive mechanical work with a 'muscular efficiency' ($\eta^{+}_{\mathrm{muscle}}$) of, on average, ~0.25 (ranging from 0.10–0.34) (Gaesser and Brooks, 1975; Margaria, 1968; Ryschon et al., 1997; Smith et al., 2005; Whipp and Wasserman, 1969) and we assumed that changes in net metabolic power would reflect the cost of the underlying plantar flexor muscle positive mechanical work replaced by the powered exoskeletons. Therefore, we multiplied changes in net metabolic power by $\eta^{+}_{\mathrm{muscle}}$=0.25 to yield the expected amount of average positive mechanical power (W kg^{-1}) delivered by the exoskeletons for a given change in net metabolic power. Then we divided the measured by the expected average positive mechanical power delivered by the exoskeletons to yield the exoskeleton performance index (i.e. ankle muscle work fraction; Eqn 1):

$$\begin{array}{c}\text{Exoskeleton}\\ \text{performance}\\ \text{index}\end{array} = \frac{\Delta\ \text{Net metabolic power} \times \eta^{+}_{\mathrm{muscle}}}{\begin{array}{c}\text{Average exoskeleton}\\ \text{positive mechanical power}\end{array}}\ . \qquad (1)$$

We inverted and scaled the performance index by $\eta^{+}_{\mathrm{muscle}}$ to obtain the 'apparent efficiency' (Asmussen and Bonde-Petersen, 1974) (Eqn 2). For example, with $\eta^{+}_{\mathrm{muscle}}$=0.25, performance index=1.0 yields 'apparent efficiency'=0.25 and would indicate that each joule of exoskeleton positive mechanical work results in a 4 joule reduction in net metabolic cost. In this case, all of the underlying ankle muscle–tendon positive work is performed by active plantar flexor fiber shortening (muscle work fraction=1.0) and none by previously stored elastic energy returned by the Achilles' tendon:

$$\begin{array}{c}\text{Ankle joint}\\ \text{muscle–tendon}\\ \text{'apparent}\\ \text{efficiency'}\end{array} = \frac{\begin{array}{c}\text{Average exoskeleton}\\ \text{positive mechanical power}\end{array}}{\Delta\ \text{Net metabolic power}} = \frac{\eta^{+}_{\mathrm{muscle}}}{\begin{array}{c}\text{Exoskeleton}\\ \text{performance}\\ \text{index}\end{array}}\ . \qquad (2)$$

It should be noted that our definition of ankle joint muscle–tendon 'apparent efficiency' allows for values >1.0. This would occur if the performance index is <$\eta^{+}_{\mathrm{muscle}}$ (i.e. muscle work fraction <$\eta^{+}_{\mathrm{muscle}}$). In fact, if all of the ankle muscle–tendon positive work was performed by Achilles' tendon recoil with small metabolic cost,

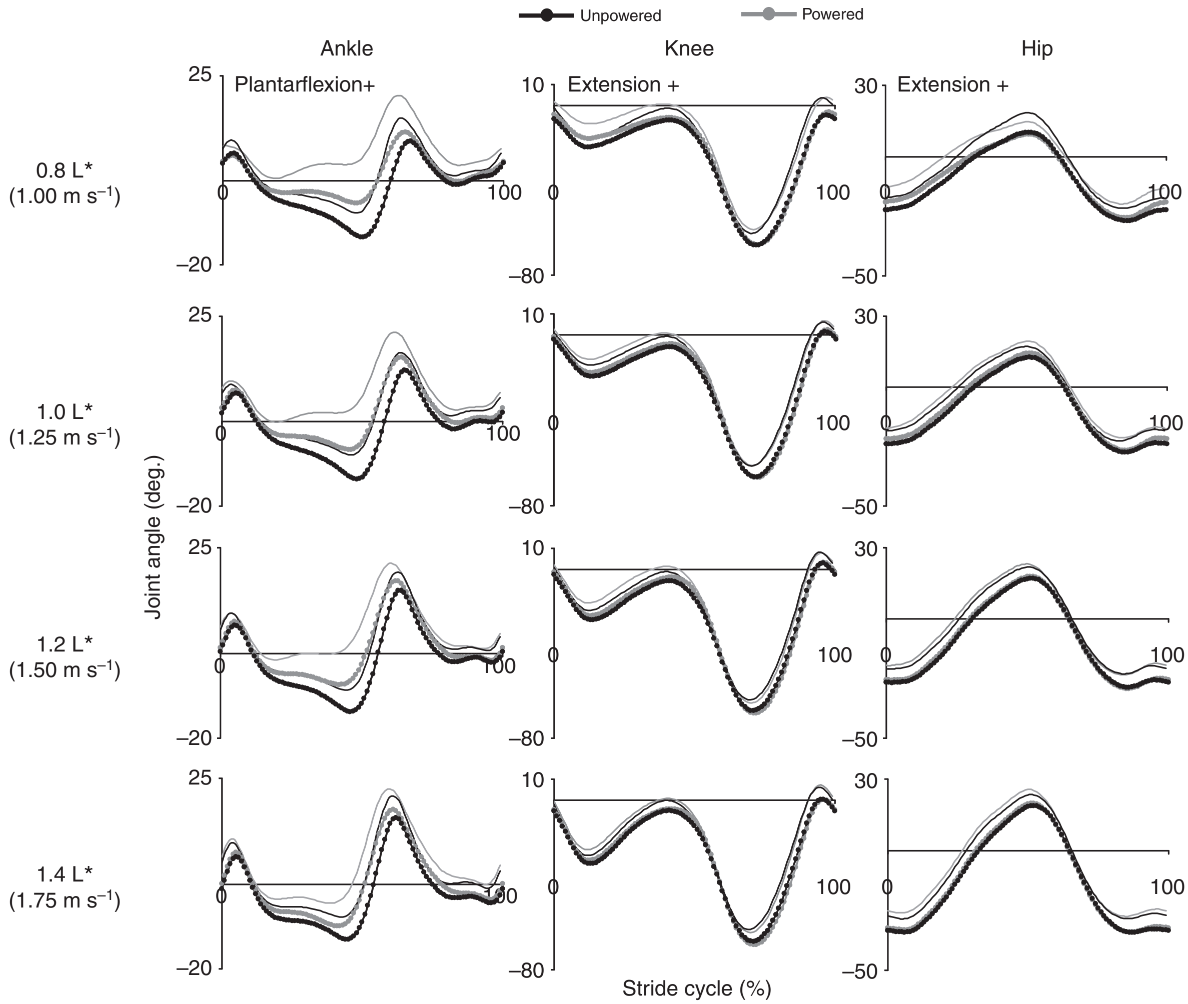

Fig. 2. Joint kinematics. The thick lines show the mean ankle (left column), knee (middle column) and hip (right column) joint angles (degrees) over the stride from heel strike (0%) to heel strike (100%) of nine subjects. Data are averages of left and right legs. Each row is walking data for a single speed/step length (0.8 L* at top to 1.4 L* at bottom). In each subplot, curves are for unpowered (black circles), and powered walking (gray circles) and thin lines are +1 s.d. Stance is ~0–60% of the stride, swing 60–100%. Ankle joint plantarflexion, knee joint extension and hip joint extension are all positive. For all joints, 0 deg. is upright standing posture.

the performance index would approach zero and the 'apparent efficiency' would approach infinity. More details on this approach can be found in our previous publication (Sawicki and Ferris, 2008).

Statistical analyses

We used JMP IN statistical software (SAS Institute, Cary, NC, USA) to perform a number of analysis of variance tests (ANOVAs). We set the significance level at $P<0.05$ for all tests. For tests that yielded significance we used *post-hoc* Tukey's honestly significant difference (THSD) tests to determine specific differences between means. For brevity, THSD results are only listed in text when not all pair-wise comparisons were significant. We also computed the statistical power of each comparison.

In the first two analyses, we assessed the effect of speed/step length (0.8 L*, 1.0 L*, 1.2 L*, 1.4 L*) on net metabolic power, exoskeleton mechanics, stance phase root mean square electromyography (r.m.s. EMG) and gait kinematics metrics [one-way ANOVA (step length)] for powered and unpowered data grouped together (except powered data only for exoskeleton mechanics and without, unpowered and powered data grouped for net metabolic power).

In the other four ANOVA analyses (one for 0.8 L*, 1.0 L*, 1.2 L* and 1.4 L*), we assessed the effect of exoskeleton mode (without, unpowered, powered), on net metabolic power (without *versus* unpowered *versus* powered), stance phase r.m.s. EMG and gait kinematics (unpowered *versus* powered) metrics [one-way ANOVA (mode)].

RESULTS

Joint kinematics

During unpowered walking, as speed/step length increased, subjects walked with increased ankle dorsiflexion, knee flexion and hip flexion early in stance phase. Push-off phase kinematics were similar across step lengths for the knee, but the ankle and hip joints were more extended for unpowered walking at longer step lengths (Fig. 2).

The knee and hip joint angles over the stride were nearly identical during powered *versus* unpowered walking for all speed/step-length conditions. Ankle joint kinematics, however, were slightly altered by exoskeleton mechanical assistance during powered walking for all speed/step-length conditions (Fig. 2).

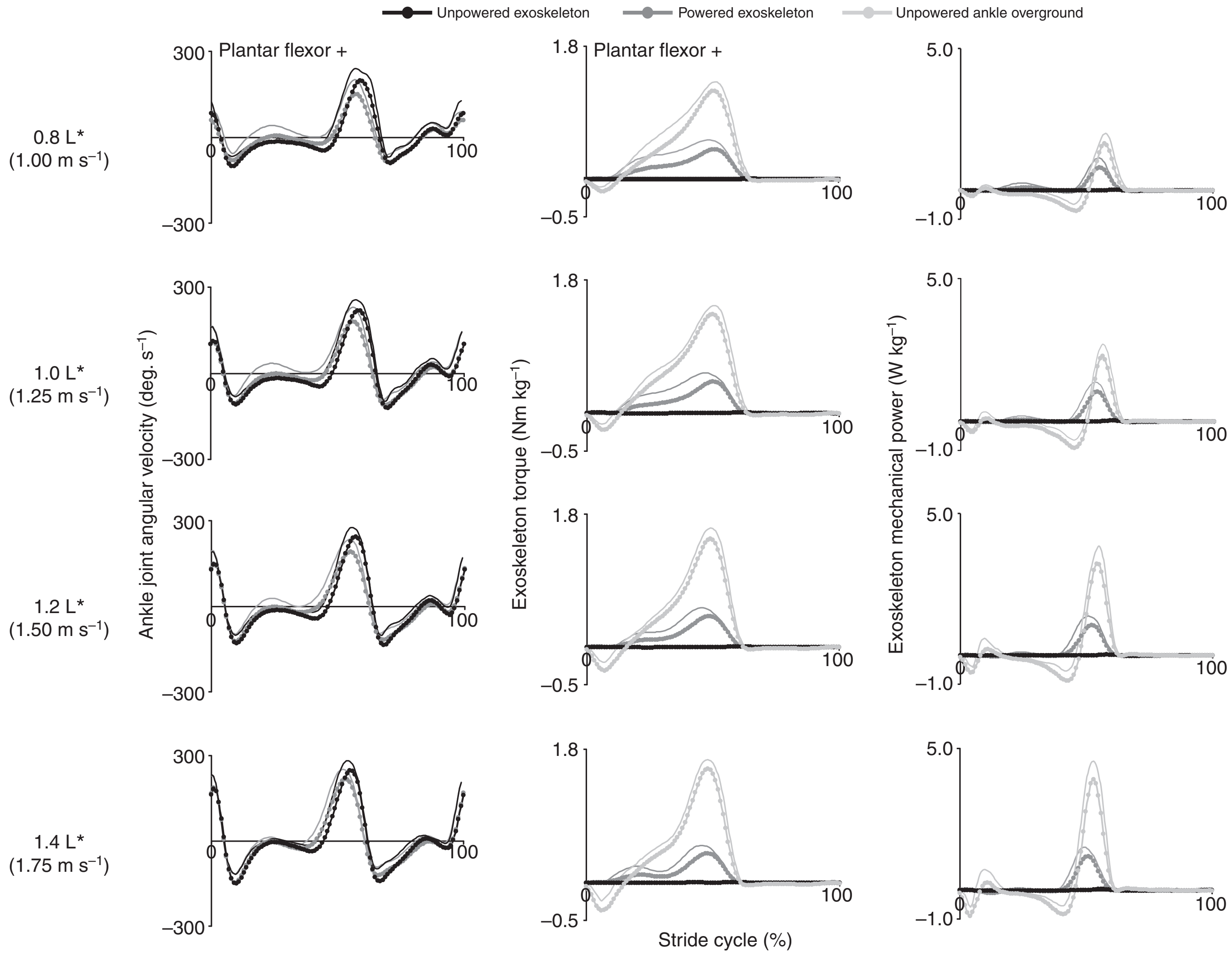

Fig. 3. Ankle exoskeleton mechanics. Thick lines show the mean ankle joint angular velocity (left column), exoskeleton torque (middle column) and exoskeleton mechanical power (right column) over the stride from heel strike (0%) to heel strike (100%) of nine subjects. Data are average of left and right legs. Each row is walking data at a single speed/step length (0.8 L* at top to 1.4 L* at bottom). In each subplot, lines are for unpowered (black circles), and powered walking (dark gray circles). Thin lines are +1 s.d. Stance is ~0–60% of the stride, swing 60–100%. Ankle joint angular velocity (deg. s^{-1}) is positive for ankle plantarflexion. Exoskeleton torque that acts to plantar flex the ankle is positive. Torque is the product of artificial muscle force and moment arm length and is normalized by subject mass (Nm kg^{-1}). Exoskeleton mechanical power is the product of exoskeleton torque and ankle joint angular velocity and is normalized by subject mass (W kg^{-1}). Positive exoskeleton mechanical power indicates transfer of energy from exoskeletons to the user's ankle muscle–tendon system. In the second and third columns, the ankle joint net muscle moment and the ankle joint mechanical power from unpowered walking overground (light gray circles) are overlaid.

Ankle joint angle was similar at heel strike but more plantar flexed throughout early stance during powered *versus* unpowered walking for all speeds/step lengths. In addition, at push-off, the ankle joint angle peak was larger and occurred earlier during stance in powered *versus* unpowered walking. For example, during unpowered 1.4 L* the ankle joint angle peaked at 62% of the stride cycle and reached ~+16°. During powered 1.4 L* the ankle joint angle peaked slightly earlier in the stride cycle and reached ~+18° (Fig. 2). For all speeds/step lengths, swing phase ankle joint angle was similar during powered and unpowered walking.

Exoskeleton mechanics

The exoskeletons produced only small amounts of torque about the ankle during unpowered walking and delivered near zero mechanical power to the user over the stride (Fig. 3).

During powered walking, exoskeletons produced similar peak torque (~0.40–0.42 Nm kg^{-1}) at all speeds/step lengths. For walking at preferred step length (1.0 L*) peak exoskeleton torque was ~32% of the overground peak ankle joint moment during unpowered walking (Fig. 3).

During powered walking, as speed/step length increased, the peak ankle joint angular velocity increased sharply and occurred earlier in the stride. Peak ankle joint angular velocity was ~154 deg. s^{-1} (at 58% of the stride) during powered 0.8 L* and increased to ~218 deg. s^{-1} (at 53% of the stride) during powered 1.4 L* (Fig. 3).

As a result of increases in ankle joint angular velocity, the peak exoskeleton mechanical power at push-off increased with speed/step length from ~0.8 W kg^{-1} during powered 0.8 L* to ~1.2 W kg^{-1} during powered 1.4 L* (Fig. 3). The exoskeleton peak mechanical power was 49% of the overground peak ankle joint mechanical power for

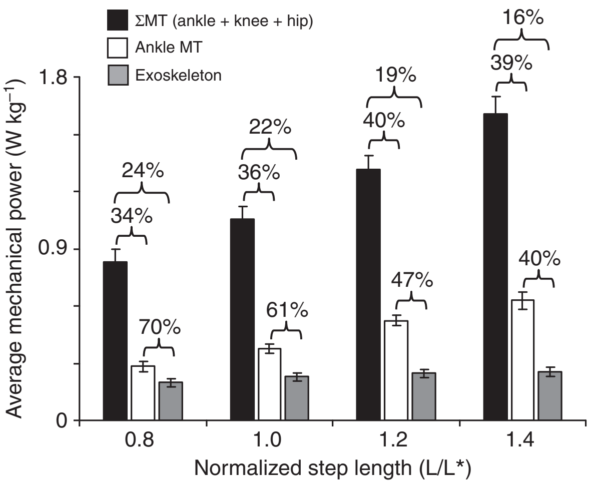

Fig. 4. Average mechanical power. Bars are the mean (N=9) average muscle–tendon (MT) positive mechanical power delivered by the sum of the ankle, knee and hip (black bars) and the ankle muscle–tendon system only (white bars) during unpowered overground walking. Gray bars are average exoskeleton positive mechanical power during powered walking on the treadmill. Error bars are ±1 s.e.m. All mechanical power values are normalized by subject mass ($\mathrm{W\,kg^{-1}}$). Speeds/step lengths increase from left 0.8 L* ($1.00\,\mathrm{m\,s^{-1}}$) to right 1.4 L* ($1.75\,\mathrm{m\,s^{-1}}$). Brackets indicate the percentage contribution of bars from right to left. For example, in the 0.8 L* condition, the exoskeleton average positive mechanical power was 70% of the ankle muscle–tendon average positive mechanical power, ankle muscle–tendon positive mechanical power was 34% of the ankle + knee + hip positive mechanical power and the exoskeleton average positive mechanical power was 24% of the ankle + knee + hip positive average positive mechanical power over the stride.

walking at the shortest step lengths (0.8 L*) and decreased to 31% of the overground peak ankle joint mechanical power for walking at the longest step lengths (1.4 L*; Fig. 3).

As speed/step length increased during powered walking, ankle exoskeletons delivered increasing absolute amounts of positive mechanical power over the stride (P=0.01, THSD, 1.4 L*>0.8 L*, 1.2 L*>0.8 L*; Fig. 3, Fig. 4, Fig. 5B). Exoskeleton average positive mechanical power was $0.20\pm0.02\,\mathrm{W\,kg^{-1}}$ (mean ± s.e.m.) during powered 0.8 L* and increased by ~25% to $0.25\pm0.02\,\mathrm{W\,kg^{-1}}$ during powered 1.4 L*. When powered, exoskeletons absorbed very little mechanical energy. Exoskeleton average negative mechanical power ($-0.03\,\mathrm{W\,kg^{-1}}$) over the stride was not different for powered walking at different step lengths (P=0.27; Fig. 5B).

Joint mechanics

As speed/step length increased during overground walking with unpowered exoskeletons, the ankle, knee and hip joint muscle–tendons combined to produce more average positive mechanical power over the stride (Fig. 4). Average ankle negative mechanical power was similar across speeds/step lengths, but the knee and hip produced more average negative mechanical power over the stride as speed/step length increased (not shown).

During overground walking with unpowered exoskeletons, the hip and ankle produced most of the positive mechanical power at all speeds/step lengths. The hip average positive mechanical power over the stride was $0.39\pm0.04\,\mathrm{W\,kg^{-1}}$ at unpowered 0.8 L*, $0.47\pm0.05\,\mathrm{W\,kg^{-1}}$ at unpowered 1.0 L*, $0.51\pm0.04\,\mathrm{W\,kg^{-1}}$ at unpowered 1.2 L*, and $0.60\pm0.04\,\mathrm{W\,kg^{-1}}$ at unpowered 1.4 L*. The ankle average positive mechanical power over the stride was $0.28\pm0.03\,\mathrm{W\,kg^{-1}}$ at unpowered 0.8 L*, $0.38\pm0.03\,\mathrm{W\,kg^{-1}}$ at unpowered 1.0 L*, $0.52\pm0.03\,\mathrm{W\,kg^{-1}}$ at unpowered 1.2 L*, and $0.63\pm0.04\,\mathrm{W\,kg^{-1}}$ at unpowered 1.4 L*.

The ankle muscle–tendon system contributed a larger percentage of the summed lower-limb muscle–tendon (ankle + knee + hip) average positive mechanical power over the stride as speed/step length increased (34% at 0.8 L* and 39% at 1.4 L*; Fig. 4). However, the exoskeletons contributed a smaller percentage of the ankle muscle–tendon positive mechanical power with increasing step length [70% at the shortest steps (0.8 L*) and only 40% at the longest steps (1.4 L*)] (Fig. 4). As a result, the exoskeletons delivered less of the average lower-limb positive mechanical power over the stride during powered 1.4 L* (16%) when compared to powered 0.8 L* (24%; Fig. 4).

Metabolic cost

Subjects' net metabolic power increased consistently with increasing speed/step length (P<0.0001). In addition, net metabolic power was significantly lower during powered *versus* unpowered walking for speeds/step lengths equal to or longer than preferred 1.0 L* (Table 1).

Probably as a result of added exoskeleton mass, the net metabolic power was significantly higher (by ~8–15%) during walking with unpowered exoskeletons compared with walking without exoskeletons for all speeds/step lengths except the longest 1.4 L* (Table 1). The net metabolic power during powered exoskeleton walking ($6.19\pm0.29\,\mathrm{W\,kg^{-1}}$) was significantly lower than for walking without wearing exoskeletons ($7.18\pm0.50\,\mathrm{W\,kg^{-1}}$) for the longest step-length condition (Table 1).

The absolute reduction in net metabolic power in powered *versus* unpowered walking increased with increasing speed/step length (P=0.002, THSD; 1.4 L*<0.8 L*, 1.2 L*<0.8 L*; Fig. 5A). At the shortest step lengths (0.8 L*), net metabolic power was $0.21\pm0.06\,\mathrm{W\,kg^{-1}}$ less during powered *versus* unpowered walking. At 1.4 L* the reduction in net metabolic power resulting from mechanical assistance was $0.70\pm0.12\,\mathrm{W\,kg^{-1}}$ (~233% more than for shortest steps). Although reductions in net metabolic power during powered walking were larger for walking with faster speeds/longer steps, relative changes in net metabolic power were similar between speeds/step lengths (8–12% reduction comparing powered to unpowered; Fig. 5A).

Table 1. Net metabolic power ($\mathrm{W\,kg^{-1}}$)

Speed/step length	Without	Unpowered	Powered	Mode P value (THSD)
0.8 L* ($1.00\,\mathrm{m\,s^{-1}}$)	2.49±0.14	2.86±0.07	2.65±0.12	P=0.008* WO<UNPOW
1.0 L* ($1.25\,\mathrm{m\,s^{-1}}$)	3.13±0.13	3.39±0.11	3.00±0.10	P=0.001* WO<UNPOW POW<UNPOW
1.2 L* ($1.50\,\mathrm{m\,s^{-1}}$)	4.22±0.18	4.62±0.22	4.04±0.13	P=0.001* WO<UNPOW POW<UNPOW
1.4 L* ($1.75\,\mathrm{m\,s^{-1}}$)	7.18±0.50	6.89±0.32	6.19±0.29	P=0.003* POW<UNPOW POW<WO

Values are means ± s.e.m., N=9; see Materials and methods for calculations.

Mode: WO, without exoskeletons; UNPOW, unpowered exoskeletons; POW, powered exoskeletons. THSD, Tukey's honestly significant difference. L*, preferred step length at $1.25\,\mathrm{m\,s^{-1}}$. P<0.05 indicates statistical significance. *Statistical power >0.80.

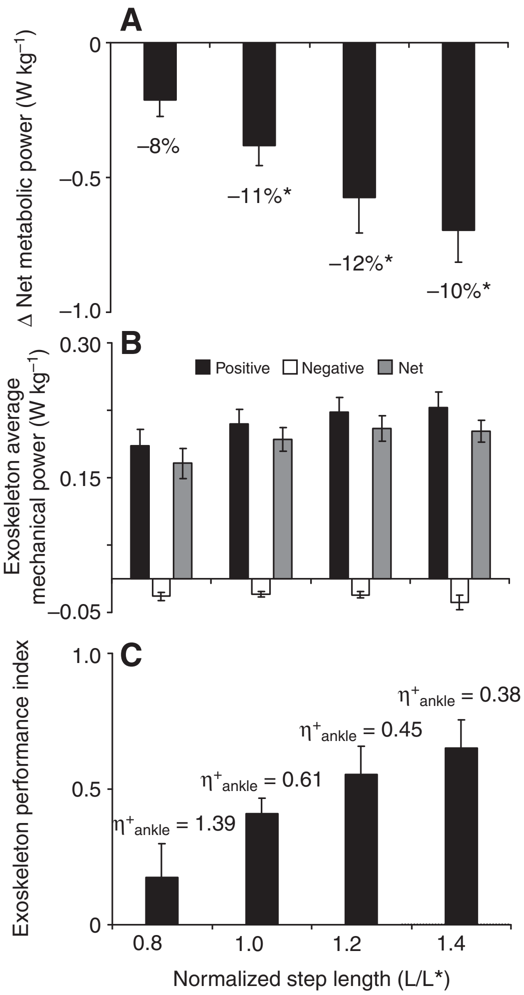

Fig. 5. Exoskeleton performance. Bars indicate nine subject means. Error bars are ±1 s.e.m. (A) Change in net metabolic power (powered–unpowered; $W\,kg^{-1}$) as a result of powered assistance from bilateral ankle exoskeletons. Values listed below bars indicate percentage difference in net metabolic power for powered *versus* unpowered walking in each condition. Asterisks indicate statistical significance for comparison of powered *versus* unpowered net metabolic power (P<0.05). (B) Exoskeleton average positive (black), negative (white) and net (dark gray) mechanical power ($W\,kg^{-1}$) over a stride for powered walking. (C) Exoskeleton performance index. Performance index (unitless) indicates the fraction of ankle muscle–tendon positive work performed by plantar flexor muscle shortening rather than Achilles' tendon recoil (i.e. muscle work fraction). Numbers listed above bars are equivalent ankle muscle–tendon 'apparent efficiency' values (see Material and methods for details). For all panels, speeds/step lengths increase from left 0.8 L* (1.00 $m\,s^{-1}$) to right 1.4 L* (1.75 $m\,s^{-1}$).

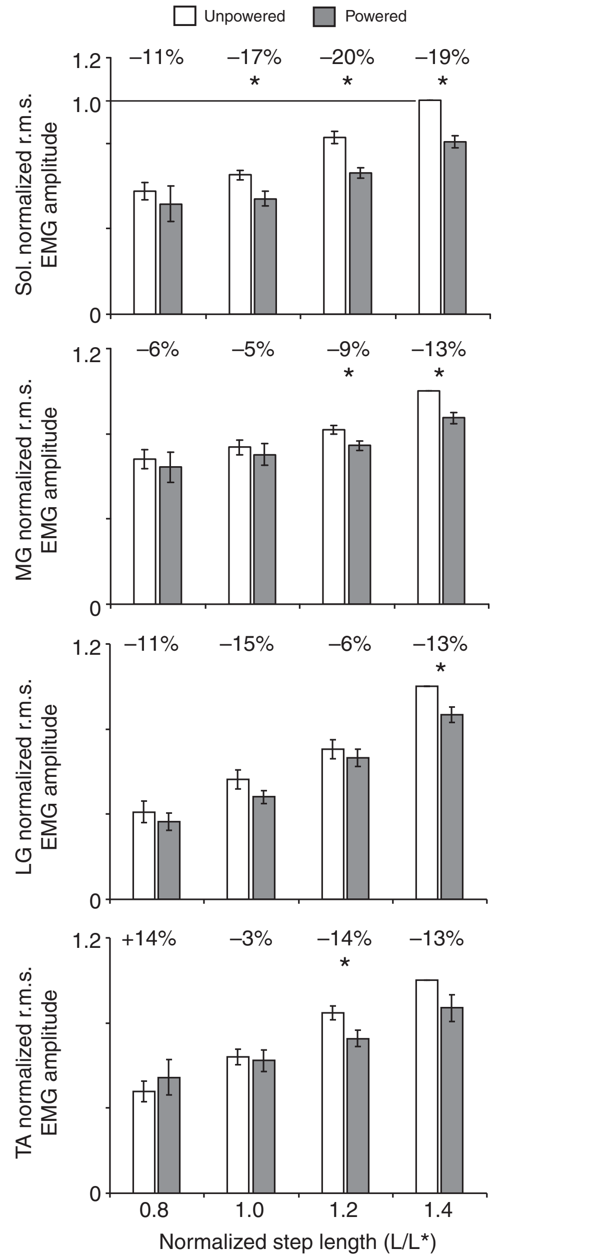

Fig. 6. Ankle muscle root mean square electromyography. Subplots are soleus (Sol.; top), medial gastrocnemius (MG), lateral gastrocnemius (LG) and tibialis anterior (TA; bottom). In each subplot, bars are normalized mean stance phase root mean square (r.m.s.) average muscle activation of nine subjects. All r.m.s. values (unitless) are normalized to the unpowered 1.4 L* condition. Error bars are ±1 s.e.m. Speeds/step lengths increase from left (0.8 L*; 1.00 $m\,s^{-1}$) to right (1.4 L*; 1.75 $m\,s^{-1}$) with unpowered walking (minutes 4–6) shown as white bars and powered walking (minutes 4–6) shown as gray bars. Numbers listed above bars indicate percentage difference in powered compared with unpowered condition. Asterisks indicate a statistically significant difference between powered and unpowered walking (P<0.05).

Exoskeleton performance index and ankle joint muscle–tendon 'apparent efficiency'

Exoskeleton performance index (i.e. ankle muscle work fraction) increased with increasing speed/step length (P=0.01, THSD; 1.4 L*>0.8 L*; Fig. 5C). Performance index increased 261% from 0.18±0.12 (ankle joint muscle–tendon 'apparent efficiency'=1.39) during powered 0.8 L* to 0.65±0.10 (ankle joint muscle–tendon 'apparent efficiency'=0.38) during powered 1.4 L*. For powered 1.0 L* and powered 1.2 L* the performance index was 0.41±0.06 (ankle joint muscle–tendon 'apparent efficiency'=0.61) and 0.56±0.10 (ankle joint muscle–tendon 'apparent efficiency'=0.45), respectively.

Electromyography

Subjects consistently increased activation of the triceps surae muscle group (i.e. soleus, medial and lateral gastrocnemius) as speed/step length increased. Soleus stance phase root mean square (r.m.s.) electromyography (EMG) was ~42% greater during unpowered and ~56% greater during powered walking at 1.4 L* when compared with walking at 0.8 L* (P<0.0001; Fig. 6). Medial and lateral gastrocnemius stance phase r.m.s. EMG both increased (by ~47% and 144%, respectively) as step length increased from 0.8 L* to 1.4 L* during unpowered walking (Fig. 6). For powered walking, medial gastrocnemius stance phase r.m.s. EMG increased by ~36% and lateral gastrocnemius stance phase r.m.s. EMG increased ~135% as speed/step length increased from 0.8 L* to 1.4 L* (P<0.0001; Fig. 6).

Subjects altered soleus muscle activation amplitude but not timing during the stance phase of powered walking when compared to unpowered walking in all speed/step length conditions. For slow walking with short steps (0.8 L*) soleus stance phase r.m.s. EMG was only ~11% lower during powered *versus* unpowered walking and the difference was not significant (0.8 L*, P=0.28; Fig. 6). At faster speeds with longer steps, reductions in soleus stance r.m.s. EMG in the powered *versus* unpowered mode were larger (~17–20%; 1.0 L*, P=0.002; 1.2 L* and 1.4 L*, P<0.0001; Fig. 6).

Reductions in both medial and lateral gastrocnemius stance phase r.m.s. EMG amplitudes during powered *versus* unpowered walking were smaller (ranging from ~6–15%) than in soleus. For medial gastrocnemius, stance phase r.m.s. EMG was reduced in powered *versus* unpowered walking only at the longest step-length conditions (1.2 L*, P=0.009; 1.4 L*, P=0.002). In the longest step-length condition, lateral gastrocnemius stance phase r.m.s. EMG was reduced during powered walking (1.4 L*, P=0.006; Fig. 6).

Tibialis anterior muscle recruitment increased with increasing speed/step length (P<0.0001) but was not significantly altered when exoskeletons were powered, except during walking at 1.2 L* (P=0.003; Fig. 6).

Gait kinematics

As expected, step length increased significantly from condition to condition (P<0.0001) and step period was the same for all step-length conditions (P=0.13; Table 2). In addition, subjects took wider steps (P<0.002) and spent less time in double support (P<0.0001) as speed/step length increased (P<0.002; Table 2).

There were no significant differences in step period (P>0.47), step width (P>0.37), or double support time (P>0.27), between powered and unpowered walking at any step length. Step length was shorter by ~1% during powered walking at 1.0 L* (P=0.04; Table 2).

DISCUSSION

Our results suggest that as speed/step length increased from 80% to 140% of the preferred step length (1.00–1.75 $\mathrm{m\,s^{-1}}$) the metabolic cost of ankle muscle–tendon positive mechanical work increased from 7% to 26% of the total metabolic cost of walking. The increased metabolic cost of ankle muscle–tendon positive work is due to a small increase in the relative contribution of the plantar flexor muscle–tendons to the total lower-limb muscle–tendon positive mechanical work (from 34% to 40%), and a large decrease in the 'apparent efficiency' of the ankle joint muscle–tendon system (from 1.39 to 0.38) with increasing speed/step length.

With powered ankle exoskeletons, subjects saved more than three times the absolute net metabolic power ($\mathrm{W\,kg^{-1}}$) in the longest (1.4 L*) compared with the shortest (0.8 L*) step-length condition, but relative reductions in metabolic cost were similar across speeds/step lengths (8–12%; Fig. 5A). This was because exoskeletons performed a progressively smaller percentage of ankle muscle–tendon (and total lower-limb muscle–tendon) average positive mechanical power at faster speeds with longer step lengths (Figs 3 and 4). Normally the human ankle muscle–tendon system generates more positive mechanical power during push-off as walking speed increases by increasing the magnitudes of both the ankle joint plantar flexor moment and the ankle joint plantar flexor angular velocity (Craik and Oatis, 1995; Winter, 1984). In the present study, although the ankle joint angular velocity increased near push-off with increasing walking speed/step length, the peak torque generated by the exoskeletons was very similar across speeds/step lengths. Increases in exoskeleton average mechanical power were due almost entirely to increases in ankle joint angular velocity. Exoskeletons delivered more average mechanical power over the stride with increasing speed/step length, but they could not match the magnitude of the increases in the biological ankle joint moment with speed/step length.

The validity of our estimates for both the relative metabolic cost (% of total cost of walking) and the 'apparent efficiency' of ankle muscle–tendon positive work depends on a key assumption. We based our calculations on the expectation that changes in subjects' net metabolic power could be attributed to powered exoskeleton mechanical work directly replacing a portion of the ankle muscle–tendon positive mechanical work during push-off. There are a number of factors that could have influenced the validity of this assumption.

Subjects could have increased their total average external mechanical power in response to exoskeleton mechanical assistance. A higher average external mechanical power during powered *versus* unpowered walking would indicate that subjects used exoskeleton energy to augment rather than replace biological muscle–tendon positive mechanical work. This would make it difficult to attribute changes in subjects' net metabolic power to exoskeleton assistance isolated at the ankle joint rather than to differences in overall gait characteristics. Net metabolic power during walking increases with increasing speed/step length (Donelan et al., 2002a), step frequency (Bertram and Ruina, 2001), and step width (Donelan et al., 2001).

Table 2. Gait kinematics during exoskeleton walking

Metric	0.8 L* UNPOW	0.8 L* POW	1.0 L* UNPOW	1.0 L* POW	1.2 L* UNPOW	1.2 L* POW	1.4 L* UNPOW	1.4 L* POW	Speed/step length P value (THSD)
Step length (mm)	572±6	565±9	723±8	715±10	854±12	841±13	980±12	967±9	P<0.0001* 1.4>1.2,1.0,0.8 1.2>1.0,0.8 1.0>0.8
Step width (mm)	123±8	127±12	111±10	111±12	107±6	113±10	123±11	125±9	P=0.002* 1.4>1.2,1.0,0.8 1.2<0.8 1.0<0.8
Step period (ms)	570±5	570±6	570±5	570±6	568±6	565±6	568±5	566±4	P=0.13
Double support period (ms)	146±5	144±5	132±5	133±5	116±4	117±3	106±3	106±4	P<0.0001* 1.4<1.2,1.0,0.8 1.2<1.0,0.8 1.0<0.8

Values are means ± s.e.m., N=9; see Materials and methods for calculations.

UNPOW, unpowered exoskeletons; POW, powered exoskeletons. Step length (speed): 0.8 L* (1.00 $\mathrm{m\,s^{-1}}$), 1.0 L* (1.25 $\mathrm{m\,s^{-1}}$), 1.2 L* (1.50 $\mathrm{m\,s^{-1}}$), 1.4 L* (1.75 $\mathrm{m\,s^{-1}}$). L* is preferred step length at 1.25 $\mathrm{m\,s^{-1}}$.

P<0.05 indicates statistical significance. *Statistical power >0.80. THSD, Tukey's honestly significant difference.

We held step frequency constant (using a metronome) and used treadmill belt speed to vary the step length (Table 2). Keeping step length and step frequency constant highly constrains the average external mechanical power to be similar for unpowered and powered walking. We also measured step width and found no differences between unpowered and powered walking during any step-length condition (Table 2).

Even with nearly constant external average mechanical power, subjects still could have altered the distribution of mechanical power across the joints between unpowered and powered walking. For example, during powered walking, increased ankle muscle–tendon positive mechanical power could have been offset by compensatory muscle–tendon mechanical power at the knee or hip. In this study, subjects were limited to walking on a motorized treadmill during powered conditions because of the tethered pneumatic hoses connecting exoskeleton artificial pneumatic muscles to a pressurized air source. Since our treadmill was not instrumented with force platforms, we could not compare joint powers using inverse dynamics for unpowered and powered walking to rule out redistribution of mechanical power. However, recent results from our lab indicate no difference in total ankle joint moment patterns when comparing powered and unpowered exoskeleton walking (Lewis et al., 2008).

Our joint kinematic and electromyography data provide good evidence that subjects did not redistribute joint mechanical power as a result of mechanical assistance from the exoskeletons. During powered walking, the ankle joint was slightly more plantar flexed during stance, but the knee and hip joint kinematics were nearly identical for powered and unpowered walking (Fig. 2). Furthermore, in the current study during powered walking, the exoskeletons delivered 32% of the peak ankle muscle–tendon moment and 48% of the peak ankle muscle–tendon mechanical power observed during overground unpowered walking trials. In response, subjects significantly decreased muscle activity in their ankle plantar flexors. Reductions in plantar flexor r.m.s. EMG provides additional support for the idea that the total ankle joint moment (and presumably mechanical power) was maintained between unpowered and powered conditions.

Reductions in soleus r.m.s. EMG (maximum of 20%) were larger than in medial gastrocnemius (maximum of 13%) and lateral gastrocnemius (maximum of 15%; Fig. 6). The larger reductions in soleus are consistent with our previous research using powered exoskeletons (20–30% reductions) (Cain et al., 2007; Gordon and Ferris, 2007; Sawicki and Ferris, 2008). It is possible that reductions in the biarticular gastrocnemius muscles due to powered assistance were smaller than in soleus because of their functional role in assisting with swing leg initiation (Meinders et al., 1998; Neptune et al., 2001) or in transferring mechanical energy from proximal muscle–tendons (Zajac et al., 2002). Another possibility is that the neural mechanism behind soleus muscle activation is fundamentally different than for medial gastrocnemius and lateral gastrocnemius (e.g. feedback *versus* feedforward dominated). Recent evidence indicates that positive force feedback *via* type Ib afferents contributes significantly to soleus muscle activity (Grey et al., 2007) and suggests that reductions in soleus muscle activity during powered *versus* unpowered walking may reflect reduced positive force feedback due to partial unloading of the Achilles' tendon.

Subjects could also have responded to added ankle joint mechanical power by increasing dorsiflexor activation. Muscle co-activation is an indicator of simultaneous positive and negative muscle–tendon work and can significantly increase the metabolic cost of walking (Winter, 1990). To address this possibility, we recorded tibialis anterior (the major ankle dorsiflexor) surface electromyography, for both unpowered and powered walking at each speed/step length (Fig. 6). Tibialis anterior r.m.s. EMG was not elevated during powered walking at any of the speeds/step lengths we tested. Although we did not measure EMG to check for co-activation at more proximal joints, our previous research has indicated no differences in the vastii, rectus femoris, and medial hamstrings between powered and unpowered ankle exoskeleton walking (Gordon and Ferris, 2007).

Finally, we also assumed that mechanical work performed by the net ankle muscle–tendon moment is an accurate estimate of the underlying mechanical work performed by the ankle plantar flexor muscles and Achilles' tendon recoil during the push-off phase of walking. The biarticular gastrocnemius muscles can theoretically transfer mechanical energy to and from the ankle joint *via* the knee and/or hip (Neptune et al., 2004a; Zajac et al., 2002). However, according to a computer simulation analysis, during the stance phase of walking the energy transfers between the knee and ankle do not significantly confound the accuracy of muscle work estimates based on net moment work (Prilutsky et al., 1996). In addition, co-activation of antagonist muscles could have confounded estimates of plantar flexor muscle work that are based on net ankle joint mechanical power. This possibility is unlikely at the ankle joint during the step-to-step transition of walking. During this phase, medial gastrocnemius and lateral gastrocnemius each perform positive work at both the ankle and knee while soleus performs positive work only at the ankle. But because there is no simultaneous negative work by ankle dorsiflexors (i.e. tibialis anterior) occurring, the positive mechanical work delivered at the ankle joint by the triceps surae (soleus, medial and lateral gastrocnemius) is all accounted for by integrating the net ankle joint mechanical power.

Given the validity of our aforementioned assumptions, our results indicate that the ankle muscle–tendon system performs positive mechanical work during walking with remarkably high 'apparent efficiency', even when increasing speed with longer step lengths. Studies indicate that actively shortening mammalian muscle fibers perform mechanical work with a 'muscular efficiency', on average, ~0.25 (0.10–0.34) (Gaesser and Brooks, 1975; Margaria, 1968; Ryschon et al., 1997; Smith et al., 2005; Whipp and Wasserman, 1969). In the current study, as walking speed/step length increased, the ankle muscle–tendon system performed positive mechanical work with lower 'apparent efficiency' (Fig. 5C). But even in the longest step-length condition (1.4 L*), the ankle was more efficient (~0.38) than muscle in isolation. These results suggest that the Achilles' tendon contributes a significant portion of the positive work performed by the ankle muscle–tendon system during walking, at all speeds/step lengths we studied.

Assuming muscle positive work is performed with $\eta^{+}_{\mathrm{muscle}}$=0.25 and accounts for the whole metabolic cost of ankle muscle–tendon work, we can compute an estimate of the upper limit on the fraction of ankle muscle–tendon positive work performed by muscles (i.e. exoskeleton performance index=ankle muscle work fraction=$\eta^{+}_{\mathrm{muscle}}/\eta^{+}_{\mathrm{ankle}}$) (Sawicki and Ferris, 2008). For walking at 0.8 L* (~1.00 m s^{-1}), we estimate that plantar flexor muscles perform at most 18% (i.e. 0.25/1.39×100) of the total ankle muscle–tendon positive work. The Achilles' tendon, therefore, must perform the remaining 82% of the ankle muscle–tendon positive work by returning previously stored elastic energy during push-off. Similarly, for walking at 1.4 L* (~1.75 m s^{-1}), we estimate that plantar flexors perform at most 66% and the Achilles' tendon at least 34% of the total ankle muscle–tendon positive work.

Our suggestion that Achilles' tendon elastic energy storage and return is significant during walking is consistent with recent *in vivo* ultrasound data from humans (Fukunaga et al., 2001; Ishikawa et al., 2005; Ishikawa et al., 2006; Lichtwark and Wilson, 2006). Ishikawa et al. showed that during walking at $1.4\,\mathrm{m\,s^{-1}}$, the soleus and medial gastrocnemius act nearly isometrically to support a 'catapult action' in the Achilles' tendon (Ishikawa et al., 2005). Negative work is stored in the triceps surae–Achilles' tendon unit over the first 70% and then released rapidly over the final 30% of the stance phase (i.e. in the push-off phase of the step-to-step transition). Rough integration of the reported mechanical power curves for the muscle–tendon unit, and the tendon only, suggests that the vast majority (>80%) of the positive work performed by the muscle–tendon during push-off is delivered by the recoiling Achilles' tendon (Ishikawa et al., 2005). Our data from similar walking speeds (1.0 L* and 1.2 L* are ~1.25 and $\sim1.5\,\mathrm{m\,s^{-1}}$) suggest that the Achilles' tendon performs at least 44–59% of the total ankle muscle–tendon work.

In vivo ultrasound experiments have not examined whether ankle muscle–tendon dynamics are altered with increasing walking step length or speed. Hof et al. used indirect methods (force platform and kinematics) to demonstrate that as walking speed (Hof et al., 2002) and step length (Hof et al., 1983) increase, soleus and gastrocnemius muscles perform a larger fraction of the ankle muscle–tendon work. We estimate from Hof's data that muscles perform ~50% of the ankle muscle–tendon positive work at $\sim1.13\,\mathrm{m\,s^{-1}}$ and ~90% at $\sim1.96\,\mathrm{m\,s^{-1}}$ (Hof et al., 1983). These increases are consistent with our calculations that the maximum ankle muscle–tendon muscle work fraction increase significantly (from ~18% to ~65%) as speed/step length increases from 0.8 L* ($\sim1.00\,\mathrm{m\,s^{-1}}$) to 1.4 L* ($\sim1.75\,\mathrm{m\,s^{-1}}$). Studies using forward dynamics computer simulations of walking also indicate that that Achilles' tendon supplies a significant amount of energy during walking and that its relative contribution is lower at higher speeds (Neptune et al., 2008; Neptune et al., 2004b; Sasaki and Neptune, 2006). Sasaki et al. showed that as simulated walking speed increases from $1.6\,\mathrm{m\,s^{-1}}$ to $2.4\,\mathrm{m\,s^{-1}}$ the fraction of positive mechanical work performed by soleus muscle fibers increases from ~50% to ~65% of the total ankle muscle–tendon positive mechanical work (Sasaki and Neptune, 2006).

Our results suggest that the relative metabolic cost of ankle muscle–tendon mechanical work increases with speed/step length during walking. The ankle muscle–tendon system provides a significant fraction of the total positive lower-limb muscle–tendon mechanical work that increases slightly with speed/step length (from 34% to 40%; Fig. 4). In addition, ankle plantar flexor muscles perform a larger fraction of the total ankle muscle–tendon positive work at faster speeds/longer step lengths, driving down the 'apparent efficiency' of ankle muscle–tendon positive work (from 1.39 to 0.38; Fig. 5C). In short, as speed/step length increases, the ankle muscle–tendon system performs a larger fraction of the total lower-limb muscle–tendon mechanical work with lower 'apparent efficiency'. Therefore, the fraction of the total net metabolic cost ($\mathrm{W\,kg^{-1}}$) of walking due to ankle muscle–tendon positive mechanical work increases at faster speeds/longer step lengths.

As step length increases from 80% to 140% of preferred, we estimate that the ankle muscle–tendon system consumes ~18% more of the total net metabolic power ($\mathrm{W\,kg^{-1}}$) during walking. For example, at 0.8 L* the percentage of the summed lower-limb muscle–tendon (ankle + knee + hip) average positive mechanical power that is delivered by the ankle muscle–tendon system is 34%. The 'apparent efficiency' lower-limb muscle–tendon positive mechanical work at 0.8 L* is 0.29 [i.e. lower-limb muscle–tendon average positive mechanical power ($0.83\,\mathrm{W\,kg^{-1}}$)/net metabolic power ($2.86\,\mathrm{W\,kg^{-1}}$)=0.29]. The 'apparent efficiency' of only the ankle muscle–tendon positive mechanical work is 1.39. Thus, the percentage of the total net metabolic power ($\mathrm{W\,kg^{-1}}$) due to ankle muscle–tendon positive work is 34%×0.29/1.39=7%. Similar calculations can be carried out for the other speed/step-length conditions. The percentage of muscle–tendon average positive mechanical power from the ankle is 36%, 40% and 39% for the 1.0 L*–1.4 L* step-length conditions. Over the same range of step lengths, the 'apparent efficiency' of total lower-limb muscle–tendon positive mechanical work is 0.31, 0.29 and 0.23 and the ankle muscle–tendon 'apparent efficiency' is 0.61, 0.45 and 0.38. Thus, we estimate the ankle muscle–tendon system consumes 18%, 26% and 24% of the total net metabolic power ($\mathrm{W\,kg^{-1}}$) for walking as speed/step length increases from preferred ($1.25\,\mathrm{m\,s^{-1}}$) to 140% preferred ($1.75\,\mathrm{m\,s^{-1}}$).

The metabolic cost of walking may be dominated by positive muscle work at the proximal joints (i.e. hip and knee). Our results suggest that humans can save a significant amount of metabolic energy at the distal ankle joint by using previously stored Achilles' tendon elastic energy to partially power push-off during the step-to-step transition. As a result, in the worst case (i.e. 1.2 L*), the ankle muscle–tendon system consumes 26% of the total net metabolic energy but produces 40% of the total positive mechanical work during walking. So where is the remaining 74% of the metabolic energy spent? Keeping along the lines of lower-limb muscle–tendon work, we feel that the hip joint muscle–tendon system might consume a large portion of unaccounted metabolic energy. The hip supplies positive mechanical work on par with the ankle (~30–40% of the total lower-limb muscle–tendon positive work). But the morphology (i.e. long muscle fibers and short or no tendons) of the human hip may significantly reduce its 'apparent efficiency' to perform positive mechanical work. It is likely that the positive work supplied by the hip muscle–tendon system is performed almost exclusively by active muscle shortening rather than passive tendon recoil. At the preferred step length, if the combined knee/hip positive mechanical work (64% of the total) accounts for the remaining 82% of the metabolic cost of walking then we estimate the combined knee/hip muscle–tendon 'apparent efficiency' is ~0.24.

Implications and future research

From a basic science perspective, our long-term goal is to establish a joint-based relationship between the mechanics and energetics of human locomotion. We hope to be able to approximately explain the metabolic cost of human walking as the sum of the metabolic cost of muscle–tendons performing positive work at each of the lower-limb joints (ankle + knee + hip). With measurements of average positive mechanical power and the 'apparent efficiency' of positive mechanical work for muscle–tendons spanning each joint this should be possible. Therefore, future studies should examine the 'apparent efficiency' of the hip and knee muscle–tendons under various walking conditions.

The importance of elastic energy storage and return in the Achilles' tendon during walking sheds light on an alternative way to view ankle exoskeleton mechanical assistance. Even if ankle plantar flexors perform little muscular work during human walking, they must still act like struts, producing the forces necessary to support body weight and series tendon elastic energy storage and return (Griffin et al., 2003; Pontzer, 2005). This may be a useful perspective to take when trying to understand changes in net metabolic power that result from powering lower-limb joints where elastic energy cycling is important (i.e. the ankle). For example, regardless of the work that exoskeleton artificial muscles perform, the torque that they develop about the ankle reduces the forces required from biological ankle plantar flexors. Although we did not use net ankle joint muscle–tendon moment data to estimate reductions in muscle forces, it should be possible to calculate an 'apparent economy' of ankle plantar flexor force production to gain insight into the relative metabolic costs of generating muscle force *versus* performing muscle work during human walking.

Considerable effort has been placed on developing assistive devices (i.e. exoskeletons and prostheses) designed to reduce the metabolic cost of walking (Guizzo and Goldstein, 2005). From an applied science perspective, our results suggest that metabolic energy savings are likely to be much more modest than expected when using an exoskeleton to supplant muscle–tendon work at distal, compliant joints. Instead, powering joints where active muscle rather than recoiling tendon performs most of the positive mechanical work (i.e. powering the less efficient joints) may lead to larger reductions in metabolic cost (Ferris et al., 2007). Furthermore, passive devices designed to reduce isometric muscle forces during periods of tendon stretch and recoil could also be useful at relatively elastic joints (i.e. ankle).

LIST OF ABBREVIATIONS

EMG	electromyography
L*	preferred step length
r.m.s.	root mean square
Speed/step length	increasing speed by varying step length at fixed step frequency
TA	tibialis anterior
η^{+}_{ankle}	ankle muscle–tendon 'apparent efficiency' of positive mechanical work
η^{+}_{muscle}	'muscular efficiency' of positive mechanical work

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