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Mechanics and energetics of incline walking with robotic ankle exoskeletons

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SUMMARY

We examined healthy human subjects wearing robotic ankle exoskeletons to study the metabolic cost of ankle muscle–tendon work during uphill walking. The exoskeletons were powered by artificial pneumatic muscles and controlled by the user's soleus electromyography. We hypothesized that as the demand for net positive external mechanical work increased with surface gradient, the positive work delivered by ankle exoskeletons would produce greater reductions in users' metabolic cost. Nine human subjects walked at 1.25 m s^{-1} on gradients of 0%, 5%, 10% and 15%. We compared rates of O_2 consumption and CO_2 production, exoskeleton mechanics, joint kinematics, and surface electromyography between unpowered and powered exoskeleton conditions. On steeper inclines, ankle exoskeletons delivered more average positive mechanical power (*P*<0.0001; +0.37±0.03 W kg^{-1} at 15% grade and +0.23±0.02 W kg^{-1} at 0% grade) and reduced subjects' net metabolic power by more (*P*<0.0001; –0.98±0.12 W kg^{-1} at 15% grade and –0.45±0.07 W kg^{-1} at 0% grade). Soleus muscle activity was reduced by 16–25% when wearing powered exoskeletons on all surface gradients (*P*<0.0008). The 'apparent efficiency' of ankle muscle–tendon mechanical work decreased from 0.53 on level ground to 0.38 on 15% grade. This suggests a decreased contribution from previously stored Achilles' tendon elastic energy and an increased contribution from actively shortening ankle plantar flexor muscle fibers to ankle muscle–tendon positive work during walking on steep uphill inclines. Although exoskeletons delivered 61% more mechanical work at the ankle up a 15% grade compared with level walking, relative reductions in net metabolic power were similar across surface gradients (10–13%). These results suggest a shift in the relative distribution of mechanical power output to more proximal (knee and hip) joints during inclined walking.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/212/1/32/DC1

Key words: locomotion, uphill walking, incline, metabolic cost, exoskeleton, ankle, human, efficiency.

INTRODUCTION

The demand for both metabolic and mechanical energy is greater for walking uphill than for walking on the level. When humans walk on a +40% surface gradient (~+22° inclination angle) the metabolic cost of transport (J m^{-1}) is approximately sixfold greater than level walking (Margaria, 1938; Margaria, 1968). The increased metabolic demand during incline walking has a simple mechanical explanation. Mechanical work (i.e. net positive work) must be done to increase the gravitational potential energy of the body center of mass during each uphill walking step (Margaria, 1968).

Center-of-mass-based mechanical analyses and measurements of oxygen consumption have given some insight into underlying muscle–tendon function during human walking on various gradients. For steady-speed walking on the level, an equal amount of positive and negative external work is performed on the center of mass (i.e. net work is zero) (Donelan et al., 2002b). Under these conditions, some negative work can be stored as elastic energy in tendons and then returned later, contributing to overall muscle–tendon positive work (Asmussen and Bonde-Petersen, 1974; Cavagna and Kaneko, 1977; Kuo et al., 2005). As surface gradient increases, the relative amount of positive *versus* negative external mechanical work performed on the center of mass increases from 50% at 0% grade to >95% at 15% grade, making elastic energy storage and return less and less likely. In fact, for walking uphill on very steep inclines (>15% grade) virtually zero negative external work is performed on the center of mass (Minetti et al., 1993) and the muscle–tendons of the lower-limb perform exclusively positive mechanical work. This is reflected in the close agreement between the efficiency of positive mechanical work performed by mammalian skeletal muscles (~0.10–0.34) (Gaesser and Brooks, 1975; Ryschon et al., 1997; Smith et al., 2005; Whipp and Wasserman, 1969) and the efficiency of positive external mechanical work performed by muscle–tendons on the center of mass on steep uphill grades (~0.25 at >20% grade) (Davies and Barnes, 1972; Margaria, 1968). One limitation of center-of-mass-based mechanical analyses is they cannot separate total lower-limb mechanical energy absorption and generation into contributions from muscle–tendons spanning each of the joints (e.g. ankle, knee and hip).

In humans, joint-based mechanical analyses (e.g. inverse dynamics) have given some insight into the distribution of mechanical energy sources across the lower-limb during uphill locomotion. Roberts et al. computed muscle–tendon work from inverse dynamics mechanical power curves collected from running humans on surfaces of increasing uphill gradient (Roberts and Belliveau, 2005). The ankle and knee joints functioned similarly on all inclines, and the hip joint delivered virtually all of the additional (i.e. net) positive work required to move uphill (Roberts and Belliveau, 2005). Joint moments (Lay et al., 2006) and joint powers (Lay et al., 2007; McIntosh et al., 2006) computed from inverse dynamics during uphill walking for the ankle knee and hip have been recently documented, but these studies did not quantify muscle–tendon mechanical work. Peak ankle, knee and hip joint extensor moments were 18%, 45% and 50% higher for walking at

15% grade than walking at 0% grade (Lay et al., 2006). Accompanying power curves suggest that the positive mechanical work produced by the ankle, knee and hip joint all increase with increasing surface gradient, but that the majority of the increase occurs at the hip joint (Lay et al., 2007; McIntosh et al., 2006). Trends in electromyography data also highlight the increasing importance of more proximal muscle–tendons during incline walking. Activation of muscles crossing all three lower-limb joints increases for walking up steeper slopes, but the largest increases are observed in the duration of thigh, not shank, muscle activity (Lay et al., 2007; Leroux et al., 1999).

Recent evidence from *in vivo* ultrasound measurements indicates that during level, steady-speed human walking the majority of ankle muscle–tendon positive mechanical work during push-off is delivered by the recoiling Achilles' tendon (Fukunaga et al., 2001; Ishikawa et al., 2005; Lichtwark and Wilson, 2006). Lichtwark et al. also showed that the mechanical behavior of the medial gastrocnemius–Achilles' tendon complex is not different for walking on inclined *versus* level surfaces (Lichtwark and Wilson, 2006). Although the average medial gastrocnemius fascicle length is longer for uphill *versus* level walking, Achilles' tendon stretch is still developed while in-series fascicles produce force nearly isometrically. As the muscle is deactivated near push-off, it performs a small amount of positive work at relatively slow shortening velocity while the recoiling elastic tissues simultaneously perform the majority of the total muscle–tendon positive work (Lichtwark and Wilson, 2006). These ultrasound studies elegantly uncover the mechanical behavior of the ankle joint muscle–tendon system during walking, but do not explicitly decipher the relative contributions of active muscle shortening *versus* previously stored tendon elastic energy to overall muscle–tendon positive work. In addition, no attempt is made to link muscle–tendon mechanics with metabolic energy expenditure.

The overall objective of the present study was to examine the mechanics and energetics of the human ankle muscle–tendon system under the demands of increasing external mechanical workload due to increasing surface incline. We used bilateral pneumatically powered ankle exoskeletons under soleus proportional myoelectric control to directly alter joint mechanics (Sawicki and Ferris, 2008; Sawicki and Ferris, 2009) and answer two questions. (1) Can powered assistance at the ankle joint reduce the metabolic cost of uphill walking? And, (2) what is the 'apparent efficiency' (Asmussen and Bonde-Petersen, 1974) of ankle muscle–tendon positive mechanical work during uphill walking? We hypothesized that as surface incline increased, exoskeletons would deliver more average positive mechanical power and subjects' net metabolic power would decrease by more than on the level. Furthermore, if ankle plantar flexor muscle fibers, rather than recoiling Achilles' tendon, perform more positive ankle muscle–tendon work on steeper inclines, then the 'apparent efficiency' of ankle muscle–tendon positive work should decrease as surface gradient increases. We also expected reduced activation amplitudes in muscles of the triceps surae group during powered walking compared to unpowered walking on all gradients. To test these predictions we compared subjects' net metabolic power and electromyography amplitudes during walking with exoskeletons powered *versus* unpowered at steady-speed on inclines of increasing uphill surface gradient. In addition, we computed the 'apparent efficiency' of ankle muscle–tendon positive work to gain insight into the relative importance of previously stored elastic energy *versus* active muscle fiber work in powering the ankle during uphill walking in humans.

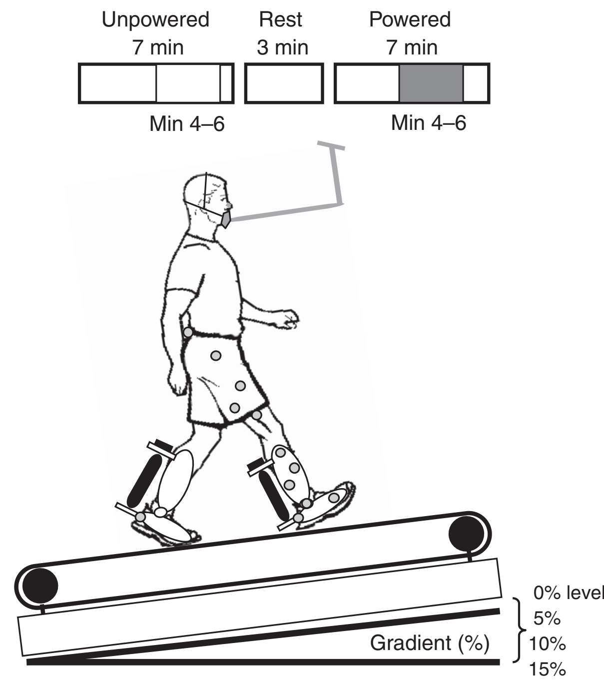

Fig. 1. Experimental set-up. Subjects walked on a motorized treadmill at $1.25\,m\,s^{-1}$ for 7 min with exoskeletons unpowered, then rested for 3 min, then walked for 7 min with exoskeletons powered at surface inclines of 0%, 5%, 10% and 15% grade presented in randomized order. Boxes indicate periods when data were collected (minutes 4–6) in both unpowered and powered conditions. During powered walking, bilateral ankle–foot orthoses (i.e. exoskeletons) were operated under proportional myoelectric control. Users' soleus muscle activity generated a real-time control signal commanding timing and amplitude of artificial pneumatic muscle forces. We used reflective markers and motion capture to collect joint kinematics, open-circuit respirometery to measure O_2 consumption and CO_2 production, surface electromyography to record ankle muscle activity and compression load transducers to record artificial muscle forces.

MATERIALS AND METHODS

Subjects

Nine (5 males, 4 females) healthy subjects (body mass= 80.3±14.7 kg; height=179±3 cm; leg length=92±2 cm) gave written, informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the University of Michigan Institutional Review Board for Human Subject research. Subjects exhibited no gait abnormalities and had practiced for at least 90 min (three or more 30 min practice sessions) previously with powered exoskeletons.

Exoskeletons

We built lightweight bilateral, ankle–foot exoskeletons (i.e. orthoses) for each subject [mass of 1.18±0.11 kg each (mean ± s.d.; Fig. 1). 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 et al., 2005). Briefly, the exoskeletons consisted of a carbon fiber shank attached to a polypropylene foot section with a metal hinge joint that allowed free rotation about the ankle dorsi/plantarflexion axis. 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 controlled exoskeleton plantar flexor torque assistance with a physiologically inspired controller that incorporated the user's own soleus electromyography to mimic the timing and amplitude of biological muscle activation (i.e. proportional myoelectric control) (Gordon and Ferris, 2007; Sawicki and Ferris, 2008; Sawicki and Ferris, 2009).

Protocol

Experienced (>90 min walking with powered exoskeletons) subjects walked at 1.25 m s^{-1} on a treadmill with bilateral powered ankle exoskeletons at four different surface inclines [0%, 5%, 10% and 15% surface gradient (i.e. 0°, 2.9°, 5.7° and 8.5° inclination angle)] during unpowered and powered exoskeleton walking (supplementary material Movie 1). Our previous research demonstrated that subjects' net metabolic power (W kg^{-1}) plateaus after 90 min of powered walking practice (Sawicki and Ferris, 2008). Subjects chose their preferred step length, step width and step frequency. Inclines were presented randomly. For each incline 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). During the unpowered bout for each surface incline, we tuned the gain and threshold of the proportional myoelectric controller so that 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). We re-tuned the controller gains for each incline so that the exoskeletons delivered similar peak torque across the powered trials independent of surface gradient. Thus, changes in average exoskeleton mechanical power output would be attributed to changes in ankle joint kinematics (range of motion, ankle joint angular velocity) rather than artificial muscle force output.

Data collection and analysis

We recorded subjects' ankle, knee and hip joint kinematics, whole-body gait kinematics, ankle dorsiflexor and plantar flexor surface electromyography, O_2 consumption and CO_2 production, and exoskeleton artificial muscle forces. For kinematic, electromyographic and artificial muscle force data, we collected 10 s trials (i.e. ~seven to nine 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 surface gradients) 7 min trials. Metabolic data were collected continuously during each 7 min trial. In addition, we collected a single 7 min quiet standing trial of metabolic data for each subject before walking trials commenced.

Specific details on procedures for analysis of the metabolic cost, kinematics, 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

We computed the exoskeleton performance index by combining measures of mechanical and metabolic power (W kg^{-1}). First, we subtracted the net metabolic power during unpowered walking from the net metabolic power during powered walking for each level of surface incline to get the metabolic power savings due to the exoskeleton assistance. Mammalian skeletal muscle performs positive mechanical work with a 'muscular efficiency' (η^+_{muscle}) of ~0.25 (0.10–0.34) (Gaesser and Brooks, 1975; Margaria, 1968; Ryschon et al., 1997; Smith et al., 2005; Whipp and Wasserman, 1969). We assumed that changes in net metabolic power would reflect the cost of the underlying plantar flexor muscle positive work replaced by the powered exoskeletons. Thus, we multiplied changes in net metabolic power by η^+_{muscle}=0.25 to yield the expected amount of positive mechanical power delivered by the exoskeletons for a given change in net metabolic power. Finally we divided the measured by the expected average positive mechanical power delivered by the exoskeletons to yield the exoskeleton performance index (Eqn 1):

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

In addition, we computed an equivalent 'apparent efficiency' (η^+_{ankle}) (Asmussen and Bonde-Petersen, 1974) by taking the reciprocal of the performance index and scaling it by η^+_{muscle} (i.e. performance index=1.0 yields 'apparent efficiency'=η^+_{muscle}; Eqn 2 below).

For example, with η^+_{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 J reduction in net metabolic cost. In this case, all of the underlying ankle muscle–tendon positive work is performed by plantar flexor muscles (muscle work fraction=1.0) and none by previously stretched Achilles' tendon.

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

'Apparent efficiency'(η^+_{ankle}) can be compared with the 'muscular efficiency' of positive mechanical work (η^+_{muscle}) to gain insight into the relative roles of muscle fiber shortening *versus* elastic tendon recoil to overall muscle–tendon positive work. More details on this approach can be found in our previous work (Sawicki and Ferris, 2008).

Statistical analyses

We performed analysis of variance tests (ANOVAs) using JMP IN statistical software (SAS Institute, Cary, NC, USA). For significant effects ($P<0.05$) we computed statistical power and 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 analysis, we assessed the effect of surface gradient (0%, 5%, 10% and 15% grade) on net metabolic power, exoskeleton mechanics, stance phase root-mean square electromyography (r.m.s. EMG) and gait kinematics metrics [one-way ANOVA (gradient)] for powered and unpowered walking data taken together (for exoskeleton mechanics metrics we analyzed powered walking data only).

In the other four ANOVA analyses (one for 0%, 5%, 10% and 15% grade), we assessed the effect of exoskeleton mode (unpowered, powered) on net metabolic power, stance phase r.m.s. EMG and gait kinematics metrics [one-way ANOVA (mode)].

RESULTS

Joint kinematics

During unpowered walking, as surface gradient increased, subjects walked with increased ankle dorsiflexion, knee flexion and hip flexion early in stance phase. Push-off phase kinematics were similar across surface gradients for all joints during unpowered walking (Fig. 2).

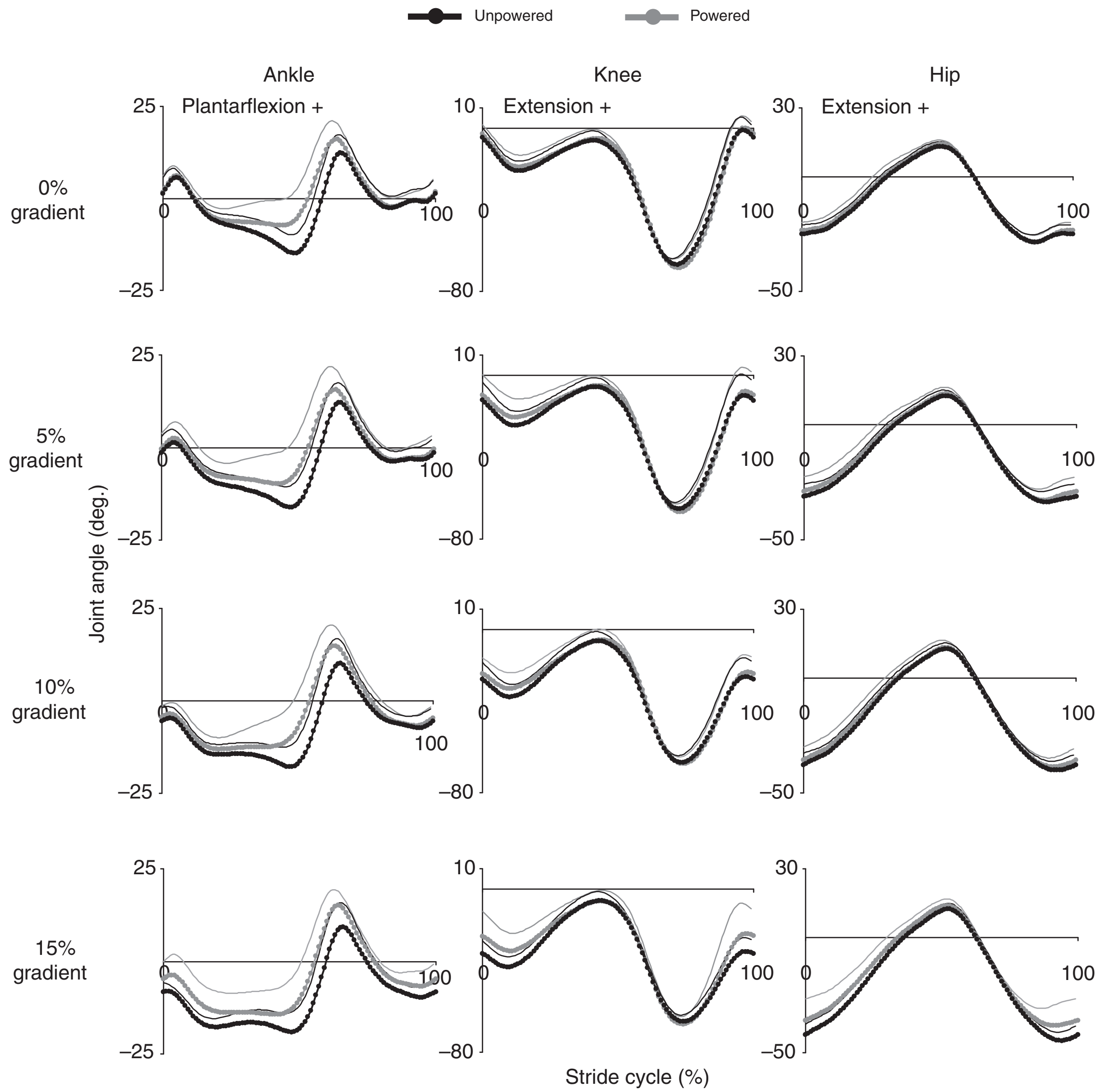

Fig. 2. Joint kinematics. Thick lines are the mean ankle (left column), knee (middle column) and hip (right column) joint angles over the stride from heel strike (0%) to heel strike (100%) of nine subjects. Data are averages of left and right legs. Each row is walking data at 1.25 $m\,s^{-1}$ on a single surface gradient (0%-level at top to 15%-uphill at bottom). In each subplot, curves are for unpowered (black circles), and powered (gray circles) walking and thin lines are +1 s.d. Stance is ~0–60% of the stride, swing 60–100%. For all joints 0 deg. is upright standing posture. Ankle joint plantarflexion, knee joint extension and hip joint extension are all positive.

Subjects adopted slightly more upright limb postures during powered *versus* unpowered walking. The ankle, knee and hip joint angles were all more extended early in stance during powered walking. This effect was more pronounced at steeper inclines (Fig. 2).

The peak ankle angle during push-off was larger (by ~3–5°) and occurred earlier in the stride cycle during powered walking than during unpowered walking at all surface gradients. Knee joint peak flexion angle and hip joint peak extension angle during push-off were similar for unpowered and powered walking on all levels of incline (Fig. 2).

Exoskeleton mechanics

During unpowered walking, the exoskeletons produced small amounts of torque about the ankle and thus delivered virtually zero mechanical power to the user (Fig. 3).

When the exoskeletons were powered, they produced ~0.40–0.48 $N\,m\,kg^{-1}$ peak torque (increasing slightly with increasing surface gradient). In addition, as surface incline increased, exoskeletons delivered increasing amounts of plantar flexor torque earlier in the stance phase (Fig. 3). For level walking, the peak exoskeleton torque during powered walking was ~33% of the peak ankle joint moment during level walking with unpowered exoskeletons at 1.25 $m\,s^{-1}$.

The peak ankle joint angular velocity during push-off increased with increasing surface gradient (+193 deg. s^{-1} during powered 0% grade and +223 deg. s^{-1} during powered 15% grade walking). Increases in exoskeleton torque and ankle joint angular velocity resulted in larger peak exoskeleton mechanical power at steeper inclines (~1.1 $W\,kg^{-1}$ on the level and ~1.3 $W\,kg^{-1}$ at 15% grade; Fig. 3). The peak

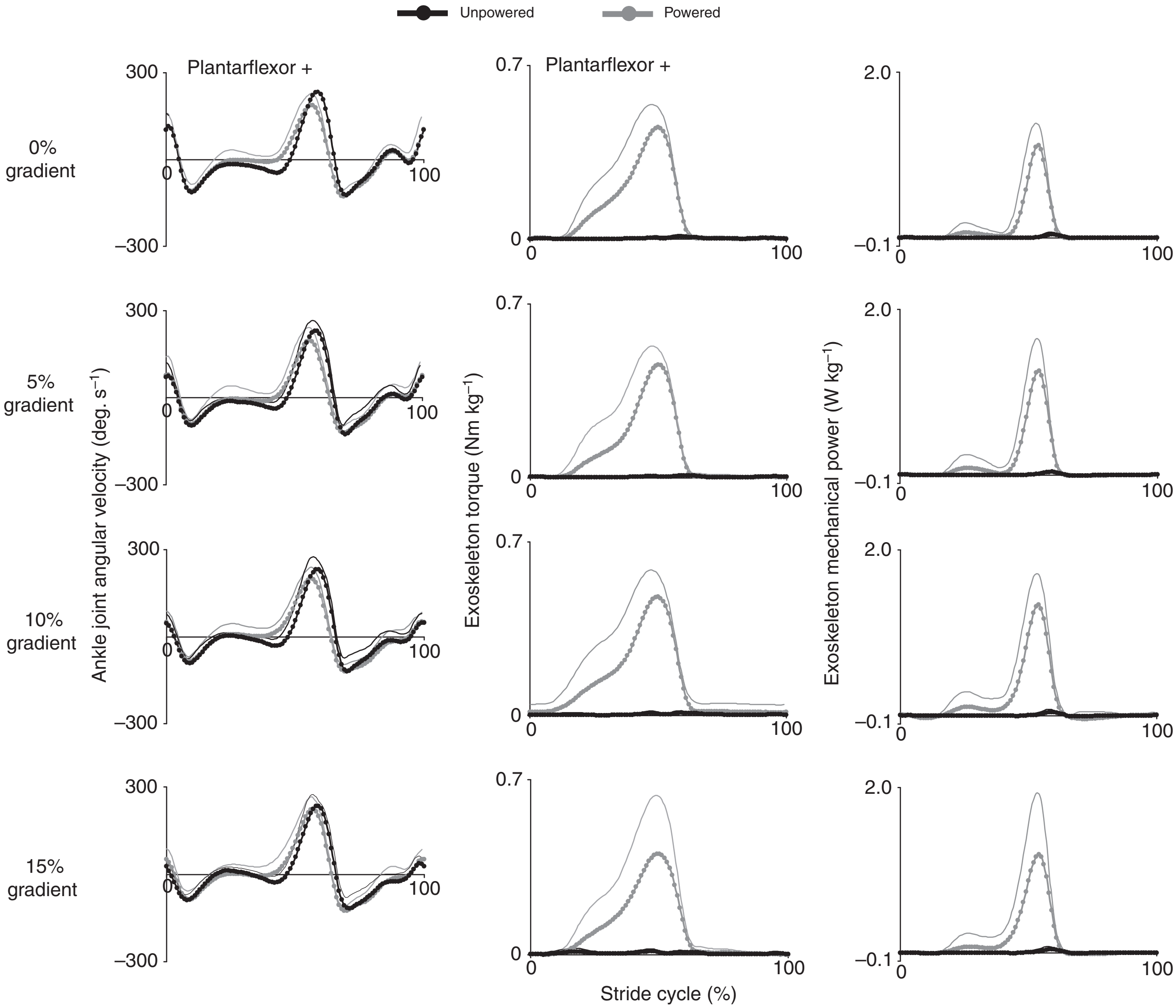

Fig. 3. Ankle exoskeleton mechanics. The thick lines are mean ankle joint angular velocity (left column), exoskeleton torque (middle column) and exoskeleton mechanical power (right column) over the stride from heel strike (0%) to heel strike (100%) of nine subjects. Data are average of left and right legs. Each row is walking data at $1.25\,\mathrm{m\,s^{-1}}$ on a single surface gradient (0%-level at top to 15%-uphill at bottom). In each subplot, bold lines are for unpowered (black circles), and powered (gray circles) walking, and thin lines are +1 s.d. Stance is ~0–60% of the stride, swing 60–100%. Ankle joint angular velocity ($\mathrm{deg.\,s^{-1}}$) is positive for ankle plantarflexion. Exoskeleton torque that acts to plantarflex the ankle is positive. Torque is the product of artificial muscle load and moment arm length and is normalized by subject mass ($\mathrm{Nm\,kg^{-1}}$). Exoskeleton mechanical power is the product of exoskeleton torque and ankle joint angular velocity and is normalized by subject mass ($\mathrm{W\,kg^{-1}}$). Positive exoskeleton power indicates transfer of energy from exoskeletons to the user's biological ankle muscle–tendon system.

exoskeleton mechanical power was ~55% of peak ankle joint mechanical power during unpowered walking at $1.25\,\mathrm{m\,s^{-1}}$ on level ground.

Powered ankle exoskeletons delivered consistently increasing amounts of positive mechanical power over the stride with increasing surface gradient ($P<0.0001$; Fig. 4B). Exoskeleton average positive mechanical power was $0.23\pm0.02\,\mathrm{W\,kg^{-1}}$ (mean ± s.e.m.) during powered 0% grade and increased by ~61% to $0.37\pm0.03\,\mathrm{W\,kg^{-1}}$ during powered 15% grade walking. Powered exoskeletons absorbed very little mechanical energy. Exoskeleton average negative mechanical power (~–$0.02\,\mathrm{W\,kg^{-1}}$) over the stride was not different for powered walking on surfaces of different incline (P=0.52; Fig. 4B).

Metabolic cost

Subjects' net metabolic power increased consistently with increasing surface incline ($P<0.0001$). In addition, net metabolic power was significantly lower during powered *versus* unpowered walking at each surface incline (Table 1).

Subjects' absolute reduction in net metabolic power with the powered exoskeletons increased steadily with increasing surface gradient ($P<0.0001$, THSD, 15%<5%, 0%; 10%<5%, 0%; Fig. 4A). On level ground, net metabolic power was $0.45\pm0.07\,\mathrm{W\,kg^{-1}}$ less during powered *versus* unpowered walking. At 15% grade, the reduction in net metabolic power as a result of mechanical assistance was $0.98\pm0.12\,\mathrm{W\,kg^{-1}}$ (~117% more than on the level). Although reductions in net metabolic

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

Gradient	Unpowered	Powered	Mode *P*-value;THSD
0%	3.36±0.13	2.91±0.13	*P*<0.0002* POW<UNPOW
5%	5.23±0.13	4.65±0.15	*P*<0.0001* POW<UNPOW
10%	7.41±0.15	6.55±0.19	*P*<0.0001* POW<UNPOW
15%	9.79±0.23	8.80±0.26	*P*<0.0001* POW<UNPOW

Values are means ± s.e.m., *N*=9; see Materials and methods for calculations.
Mode: UNPOW, unpowered exoskeletons; POW, powered exoskeletons; *P*<0.05 indicates statistical significance; *statistical power >0.80; THSD, Tukey's honestly significant difference.

power during powered walking were larger on steeper inclines, relative changes in net metabolic power were similar between surface gradients (10–13% reduction from powered to unpowered mode; Fig. 4A).

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

Exoskeleton performance index increased with increasing surface gradient (*P*=0.02, THSD, 15%>0%; 10%>0%; Fig. 4C). Performance index (i.e. muscle work fraction) increased ~40% from 0.47±0.05 (ankle joint 'apparent efficiency'=0.53) during powered 0% grade to 0.66±0.06 (ankle joint 'apparent efficiency'=0.38) during powered 15% grade.

Electromyography

Subjects increased activation of the triceps surae muscle group (i.e. soleus, medial and lateral gastrocnemius) as surface incline increased. Soleus stance phase root mean square (r.m.s.) electromyography (EMG) was ~32% greater during unpowered and ~44% greater during powered walking at 15% grade when compared with walking on the level (*P*<0.0001, THSD, 15%>10%, 5%, 0%; 10%>0%; 5%>0%). Medial and lateral gastrocnemius stance phase r.m.s. EMG both increased by ~56% as surface gradient increased from 0% to 15% grade during unpowered walking. For powered walking, medial gastrocnemius stance phase r.m.s. EMG increased by ~58% and lateral gastrocnemius stance r.m.s. EMG increased ~77% as surface incline increased from 0% to 15% grade (*P*<0.0001; Fig. 5).

Subjects significantly altered soleus muscle activation amplitude but not timing during the stance phase of powered walking when compared with unpowered walking for all surface inclines. On the level, soleus stance phase r.m.s. EMG was ~25% less during powered *versus* unpowered walking (0% grade, *P*=0.0008). At steeper surface inclines, reductions in soleus stance r.m.s. EMG in the powered *versus* unpowered mode were smaller (~16–18%) but still significant (5–15% grade; *P*<0.0007; Fig. 5).

Similar to the soleus muscle, subjects walked with reduced lateral gastrocnemius r.m.s. EMG amplitudes during powered *versus* unpowered walking (0% grade, *P*=0.002; 5% grade, *P*=0.006; 10% grade, *P*=0.07; 15% grade, *P*=0.001). For level walking, lateral gastrocnemius activation amplitude was ~24% lower in powered *versus* unpowered exoskeleton mode and ranged from 8% to 15% lower for walking at steeper inclines (Fig. 5).

Reductions in medial gastrocnemius stance phase r.m.s. EMG during powered *versus* unpowered walking were less substantial than in soleus or lateral gastrocnemius. Medial gastrocnemius stance phase r.m.s. EMG was less during powered than unpowered walking only during the 5% grade condition (by ~11%; *P*=0.01; Fig. 5).

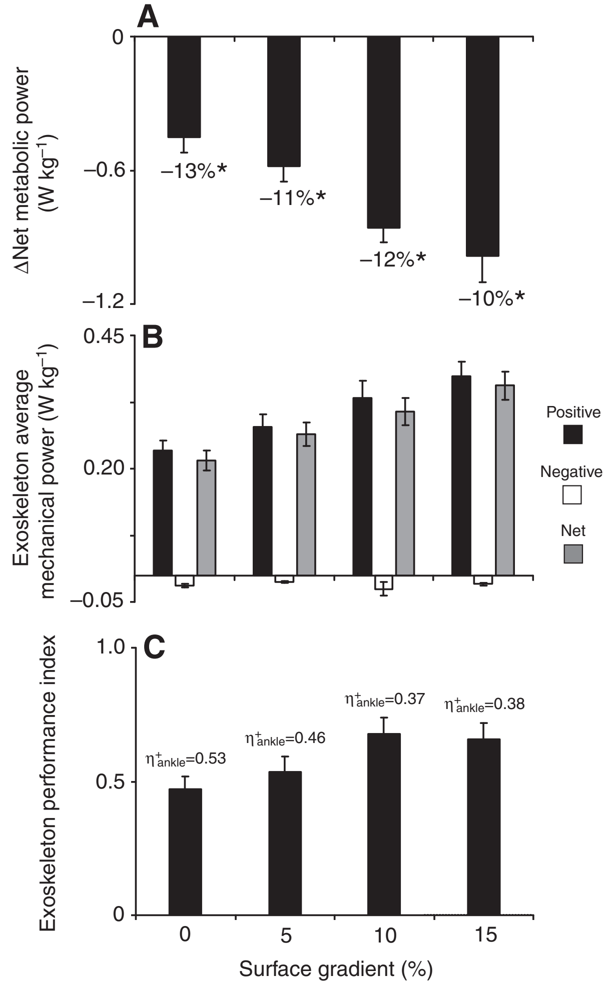

Fig. 4. Exoskeleton performance. Bar graphs show the mean (A) change in net metabolic power (powered–unpowered; $W\,kg^{-1}$) as a result of powered assistance from bilateral ankle exoskeletons, (B) exoskeleton average positive (black), negative (white) and net (dark gray) mechanical power ($W\,kg^{-1}$) over a stride for powered walking and (C) exoskeleton performance index (unitless) of the nine subjects. Performance index 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 above bars are equivalent ankle muscle–tendon 'apparent efficiency' values (see Materials and methods for details). For all panels, surface inclines increase from left (0%-level) to right (15%-uphill). Error bars are ±1 s.e.m. Asterisks (in A) indicate statistical significance for comparison of powered *versus* unpowered net metabolic power (*P*<0.05).

TA muscle recruitment did not change with increasing surface gradient (*P*=0.52) and was not significantly altered when exoskeletons were powered at any level of surface incline (*P*>0.05; Fig. 5).

Gait kinematics

Step length (*P*=0.02, THSD, 15<5%) and step period (*P*=0.04, THSD, 15<5%) were both shorter for walking at steeper inclines (unpowered and powered data pooled; Table 2). Subjects took wider steps as surface gradient increased (*P*=0.004, THSD, 15%>0%). Double support time did not change with surface gradient (*P*=0.90; Table 2).

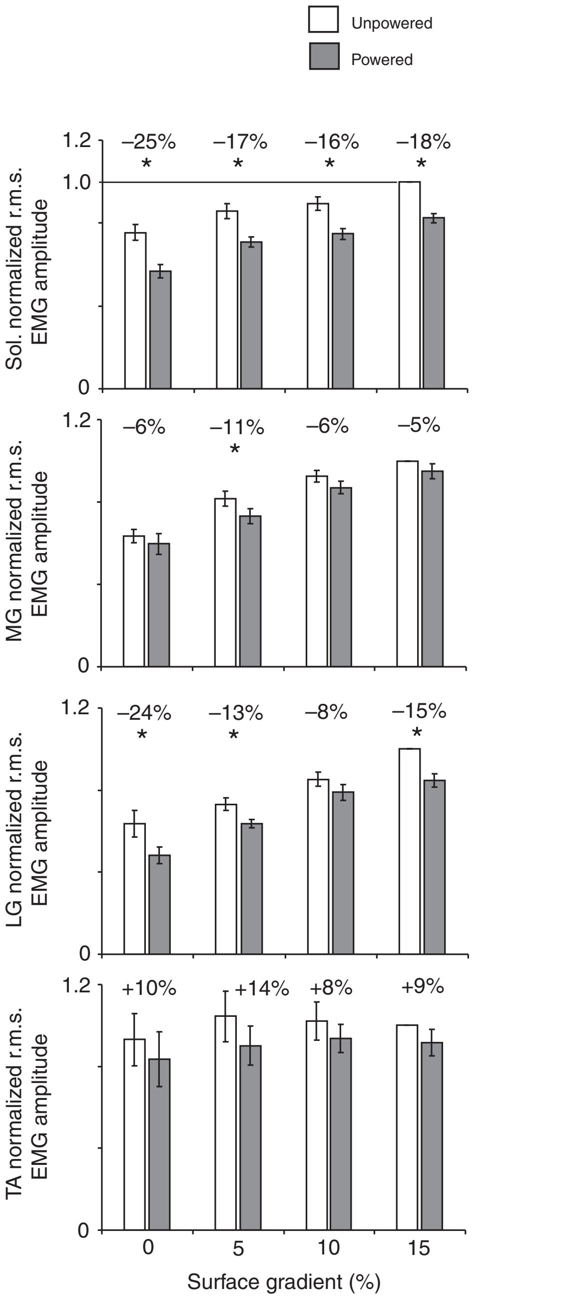

Fig. 5. Ankle muscle root mean square electromyography (EMG) for soleus (Sol.; top), medial gastrocnemius (MG), lateral gastrocnemius (LG) and tibialis anterior (TA; bottom). Values are mean stance phase root mean square (r.m.s.) average muscle activation for nine subjects (error bars are ± 1 s.e.m.). Surface gradients increase from left (0%-level) to right (15%-uphill) with unpowered walking (minutes 4–6) in white and powered walking (minutes 4–6) in gray. All r.m.s. values (unitless) are normalized to the unpowered 15% grade condition. Values above bars indicate percentage difference in powered *versus* unpowered condition. Asterisks indicate a statistically significant difference between powered and unpowered walking (ANOVA, $P<0.05$).

When comparing unpowered and powered walking, step length ($P>0.30$), step period ($P>0.75$), step width ($P>0.20$), and double support period ($P>0.39$), were not significantly different for any incline level (Table 2).

DISCUSSION

Our results indicate that the ‘apparent efficiency’ of ankle muscle–tendon positive mechanical work ($\eta^{+}_{\mathrm{ankle}}$) decreased from 0.53 to 0.38 as surface incline increased from 0% to 15% grade. Lower $\eta^{+}_{\mathrm{ankle}}$ suggests an increased contribution of actively shortening plantar flexor muscle fibers, rather than passively recoiling Achilles’ tendon, to overall ankle muscle–tendon positive work. On a 15%-uphill grade, powered ankle exoskeleton artificial muscles replaced 61% more ankle muscle–tendon work than on the level. In response, during powered walking on 15% grade, subjects decreased their absolute net metabolic power ($\mathrm{W\,kg^{-1}}$) by more than twice as much as on the level. However, the net metabolic cost ($\mathrm{W\,kg^{-1}}$) of walking was threefold greater for uphill walking on a 15% grade *versus* on the level. Reductions in net metabolic power due to powered assistance were nearly proportional to increases in net metabolic power of walking on steeper inclines. Thus, powered assistance at the ankle joint reduced the metabolic cost of walking by 10–13%, independent of surface gradient.

Our ankle muscle–tendon ‘apparent efficiency’ estimates give insight into the relative contribution of positive work performed by plantar flexor muscle fibers *versus* that delivered by previously stretched Achilles’ tendon (i.e. during recoil) to overall ankle muscle–tendon positive work output (Sawicki and Ferris, 2008; Sawicki and Ferris, 2009). In this study, for walking on surface inclines up to 15% grade, the ‘apparent efficiency’ of ankle muscle–tendon positive mechanical work was always greater than the range of reported values (0.10–0.34) for ‘muscular efficiency’ of positive mechanical work ($\eta^{+}_{\mathrm{muscle}}$) for mammalian muscle (Gaesser and Brooks, 1975; Margaria, 1968; Ryschon et al., 1997; Smith et al., 2005; Whipp and Wasserman, 1969). This suggests a significant contribution from Achilles’ tendon recoil to total ankle joint muscle–tendon positive mechanical power output, even during steep uphill walking.

The ‘apparent efficiency’, $\eta^{+}_{\mathrm{ankle}}$, of ankle muscle–tendon positive mechanical work decreased from 0.53 during level walking to 0.38 on a 15% uphill surface gradient (Fig. 4C). These values imply that active ankle plantar flexor muscle shortening provides a larger fraction of total ankle muscle–tendon positive mechanical work on a 15% grade than on the level. Based on $\eta^{+}_{\mathrm{ankle}}$ of 0.53 during level walking, and using a value of $\eta^{+}_{\mathrm{muscle}}=0.25$, we estimate that active muscle shortening accounts for ~47% of the total positive mechanical work output at the ankle (i.e. $47\%=0.25/0.53\times100$ assuming that ankle muscle–tendon metabolic energy expenditure is determined solely by the metabolic cost of ankle plantar flexor muscle positive work). This implies that previously stretched Achilles’ tendon delivers more than half (53%) of the ankle muscle–tendon positive mechanical work during level walking. Our estimates of the fraction of ankle muscle–tendon work delivered by active muscle *versus* passive Achilles’ tendon recoil for the other surface gradient conditions yield: for walking at 5% grade, 46% tendon; at 10% grade, 32% tendon; and at 15% grade, 34% tendon. Plantar flexor muscles contribute more of the ankle muscle–tendon work on steeper inclines. But despite increasing demand for net positive mechanical work, the Achilles’ tendon still contributes >30% of the ankle muscle–tendon positive mechanical work, even during steep uphill walking. Even assuming an extreme value of 0.34 for $\eta^{+}_{\mathrm{muscle}}$, at 15% grade we estimate that Achilles’ tendon recoil still contributes 11% of the total ankle muscle–tendon positive mechanical work.

Ultrasound data support our suggestion that tendon recoil is a major contributor to ankle muscle–tendon positive mechanical power during human walking on level ground and on uphill inclines. Using

Table 2. Gait kinematics during exoskeleton walking

Metric	0% gradient Unpowered	0% gradient Powered	5% gradient Unpowered	5% gradient Powered	10% gradient Unpowered	10% gradient Powered	15% gradient Unpowered	15% gradient Powered	Gradient *P* value; THSD
Step length (mm)	729±4	722±8	734±7	731±13	723±11	718±16	712±13	709±16	0.02* 15%<5%
Step width (mm)	99±12	106±13	107±12	109±11	112±11	114±8	118±9	120±6	0.004** 15%>0%
Step period (ms)	573±3	574±5	575±6	576±9	570±9	572±12	559±11	562±12	0.04* 15%<5%
Double support period (ms)	136±4	136±5	137±4	137±6	138±5	137±6	135±5	138±6	0.90

Values are means ± s.e.m., *N*=9; see Materials and methods for calculations.
P<0.05 indicates statistical significance; *statistical power >0.65; **statistical power >0.80; THSD, Tukey's honestly significant difference.

ultrasound, Lichtwark et al. showed that when humans walk on the level or uphill on a 10% surface gradient, the Achilles' tendon is stretched significantly while in series muscle fascicles produce force nearly isometrically (Lichtwark and Wilson, 2006). Tendon elastic stretch is followed by a mechanical power burst near push-off that is shared by muscle fascicles (shortening at relatively slow velocity) and recoiling elastic Achilles' tendon. These studies did not report the fraction of ankle muscle–tendon positive work performed by shortening fascicles *versus* that delivered by previously stretched recoiling Achilles' tendon.

Our estimate that shortening muscles contribute a larger percentage of the total ankle joint muscle–tendon positive work as incline increases (47% on level and 66% at 15% grade) is consistent with recent *in vivo* studies of uphill locomotion in animals. For example, as turkeys move up an inclined surface, the mechanical behavior of the lateral gastrocnemius shifts from a force-producing strut (active isometric) to a work producing motor (active shortening) in order to provide a portion of the mechanical work needed to raise the animal's center of mass (Roberts et al., 1997). More detailed studies in both turkeys (Gabaldon et al., 2004) and guinea fowl (Daley and Biewener, 2003) also demonstrate that distal leg muscles (lateral gastrocnemius, digital flexor and peroneous longus) increase net active shortening and positive mechanical work output during uphill running.

Our 'apparent efficiency' ($\eta^{+}_{\mathrm{ankle}}$) estimates depend on the validity of a key assumption: that the observed changes in metabolic cost are due to exoskeleton positive mechanical work directly replacing ankle plantar flexor muscle work (Sawicki and Ferris, 2008; Sawicki and Ferris, 2009). Subjects could have used exoskeletons to augment total lower-limb muscle–tendon work rather than to replace only ankle muscle–tendon work. In that case we would expect increases in the total lower-limb muscle–tendon average positive mechanical power during powered *versus* unpowered walking trials. During uphill walking, the external mechanical work (and net metabolic cost) both increase in proportion to both speed and surface incline (Margaria, 1938; Minetti et al., 1993). We held the treadmill speed and surface gradient constant to constrain the average external mechanical power to be similar between unpowered and powered walking trails.

Subjects' joint kinematics indicated that exoskeleton assistance altered only the ankle joint muscle–tendon mechanics. Highly constraining the external mechanical power between unpowered and powered walking does not rule out subjects' redistributing joint power output across the lower-limb joints. For example, subjects could have dissipated ankle exoskeleton positive mechanical power by delivering simultaneous negative mechanical power at the knee or hip. This did not appear to be the case. The ankle, knee and hip joint angles were all slightly more extended during powered than unpowered walking trials (Fig. 2). As a result subjects walked with a more upright posture, and slightly increased the effective mechanical advantage of the muscle–tendons spanning each of the lower-limb joints (Biewener, 1989; Biewener et al., 2004a). Greater effective mechanical advantage reduces net muscle moments, especially at proximal joints (knee, hip). Thus, if compensatory negative power was performed at the knee or hip, we would expect considerable increases in the angular velocity at those joints over the stride (i.e. power=moment×angular velocity). The hip and knee joint angles were slightly shifted (i.e. towards extension) but their slopes were similar over the entire stride, especially near push-off (Fig. 2).

Our electromyography data provide additional evidence that subjects used exoskeleton mechanical assistance to replace rather than augment ankle muscle–tendon work. The stance phase r.m.s. EMG amplitudes for all three major ankle plantar flexor muscles were lower during powered than unpowered walking (Fig. 5). The magnitudes of the observed reductions in triceps surae r.m.s. EMG were consistent with our previous studies on powered exoskeleton walking. These reductions result in a combined artificial plus biological net ankle moment that produces similar kinematics and kinetics during powered and unpowered walking (Gordon and Ferris, 2007; Lewis et al., 2008; Sawicki and Ferris, 2008; Sawicki and Ferris, 2009). This suggests that exoskeleton artificial muscles directly reduced the load on the underlying ankle plantar flexor muscle–tendon units. Reductions in soleus r.m.s. EMG (16–25%) were more pronounced than for the biarticular medial and lateral gastrocnemius (5–24%; Fig. 5). It could be that positive force feedback from Ib afferents plays a larger role in modifying soleus than gastrocnemius muscle activity during uphill walking (Grey et al., 2007). In that case, reduced loading on the Achilles' tendon as a result of exoskeleton torque assistance would reduce soleus activity by more than gastrocnemius activity.

Muscle co-activation at the ankle to stabilize the joint during powered walking could exact a significant metabolic cost and confound our measured differences in net metabolic power resulting from exoskeleton assistance. We measured muscle activity in the tibialis anterior (i.e. the major ankle dorsiflexor) to assess this possibility. Our results indicate no significant differences in tibialis anterior r.m.s. EMG amplitudes between powered and unpowered walking conditions on any surface incline (Fig. 5). This gives us confidence that ankle muscle co-activation was not a factor. Furthermore, our previous research indicates that during powered walking, muscle co-activation is not a factor at the knee or hip (Gordon and Ferris, 2007).

Walking with longer (Donelan et al., 2002a), wider (Donelan et al., 2001) or more frequent steps (Bertram and Ruina, 2001) increases the mechanical and metabolic energy expenditure of walking. Although subjects took slightly shorter, wider and higher frequency steps on steeper inclines, there were no significant differences in these gait parameters between powered and unpowered walking conditions on any surface incline (Table 2). Therefore, changes in overall gait parameters did not confound our measured changes in net metabolic power resulting from powered exoskeleton assistance.

The metabolic cost of swinging the legs is significant during human walking, accounting for up to 30% of the total metabolic cost (Doke et al., 2005; Doke and Kuo, 2007; Gottschall and Kram, 2005) and increases with added mass on the lower limbs (Browning et al., 2007). It is possible that leg swing metabolic cost accounts for a larger percentage of the total metabolic cost of walking as surface incline increases. Exoskeleton mechanical assistance might then have a smaller effect on whole-body metabolism, keeping relative changes in net metabolic power from mechanical assistance constant. We believe this is unlikely for two reasons. First, Minetti et al. showed that although the external positive work (W_{ext}+) done on the center of mass increases with increasing surface incline, the internal work done to move the limbs relative to the center of mass (W_{int}+) remains relatively constant with increasing surface incline (Minetti et al., 1993) This indicates that leg swing costs probably remain nearly constant. Second, a recent study by Doke et al. demonstrated that the cost of swinging the legs may not depend on performing mechanical work, but instead on producing force in short bursts (Doke and Kuo, 2007). That is, leg swing cost during walking should depend mainly on step frequency. In this study, subjects increased step frequency by ~2.5% as surface gradient increased from 0% grade (level) to 15% grade. Although this change was statistically significant, it is too small to appreciably affect the relative cost of leg swing to the overall metabolic cost of walking across surface inclines.

Subjects saved more absolute net metabolic power by mechanical assistance on steeper uphill gradients, but relative reductions in net metabolic power remained nearly constant at 10–13%, independent of surface gradient. This is probably a result of decreased effectiveness of the exoskeletons as the gradient increased. Increased exoskeleton average mechanical power (+61% from 0% to 15% grade; Fig. 4B) probably contributed a smaller fraction of the total ankle plus knee plus hip muscle–tendon average positive mechanical power ($W\,kg^{-1}$) on steeper inclines. A limitation of the current study was that we could not compute lower-limb joint inverse dynamics on inclined surfaces. As a result it was not possible to calculate the relative contribution of average exoskeleton positive mechanical power to the overall mechanical power produced at the ankle joint (or summed joints) as was done in our previous research (Sawicki and Ferris, 2008; Sawicki and Ferris, 2009). However, recent studies in walking and running humans (Lay et al., 2006; McIntosh et al., 2006; Roberts and Belliveau, 2005) and running animals (Biewener et al., 2004b; McGowan et al., 2007; Rubenson et al., 2006) suggest that as surface incline increases, there is a shift in the relative distribution of lower-limb positive mechanical work from the distal (e.g. ankle) to the proximal (e.g. hip and knee) muscle–tendons. If the hip and knee joint muscle–tendons perform a larger fraction of the total lower-limb (ankle + knee + hip) muscle–tendon positive mechanical work then they should also account for the majority of the total metabolic cost of uphill walking. Thus, ankle exoskeleton positive mechanical work probably influenced a smaller fraction of the total metabolic cost of walking on steeper inclines, keeping relative changes in metabolic cost independent of surface gradient.

In our previous research, during level walking at $1.25\,m\,s^{-1}$ and preferred step length, the ankle muscle–tendon system performed 36% of the total lower-limb positive mechanical work and accounted for 18% of the total metabolic cost (i.e. 36%×0.31/0.61=18%) (Sawicki and Ferris, 2009). In that case, the 'apparent efficiency' of ankle muscle–tendon positive mechanical work was 0.61 and the efficiency of total lower-limb muscle–tendon positive work (ankle + knee + hip) was 0.31. The exoskeletons delivered 61% of the total ankle muscle–tendon work and subjects reduced their net metabolic power by 11% (i.e. 0.61×18%=11%). In this study, on a 15% uphill gradient, the 'apparent efficiency' of ankle muscle–tendon positive mechanical work was 0.38 and subjects reduced their net metabolic power by 10%. If on a 15% uphill gradient the exoskeletons delivered 61% of the ankle muscle–tendon positive work (probably an overestimate) and the efficiency of total lower-limb muscle–tendon positive work (ankle + knee + hip) was 0.31 (also probably an overestimate), then with an ankle muscle–tendon 'apparent efficiency'=0.38, the ankle muscle–tendon system would have to account for ~20% of the total lower-limb positive mechanical work to explain the observed 10% reduction in metabolic cost (i.e. 61% of 20%×0.31/0.38=10%). In other words, using a very rough calculation, we estimate the relative contribution of the knee/hip muscle–tendons to summed lower-limb muscle–tendon positive mechanical work increases from 64% to ~80% as surface gradient increases from level to 15% uphill.

Finally, it is interesting to note that our ankle muscle–tendon 'apparent efficiency' values did not change much from 10% (0.37) to 15% (0.38) uphill walking gradient. It is possible that the architecture of the ankle muscle–tendon system limits its ability to modulate mechanical work output during tasks that require increased external work (e.g. uphill inclines). The idea that muscle–tendon morphology might constrain mechanical performance is not new, and has been suggested for other animals (e.g. wallabies) that have long tendons at distal joints that are probably specialized for elastic energy storage and return (Biewener et al., 2004b; McGowan et al., 2007). It would be interesting to test whether ankle muscle–tendon 'apparent efficiency' decreases further on steeper inclines (>15% uphill gradient), or if a long elastic Achilles' tendon does indeed pose a mechanical constraint.

Implications and future directions

Powered exoskeletons are a novel tool for studying the relationship between the mechanics and energetics of the lower-limb muscle–tendons during locomotion. Our research demonstrates that ankle muscle–tendon positive mechanical power is relatively cheap from a metabolic perspective. That is, for steady walking across different speeds/step lengths (Sawicki and Ferris, 2008; Sawicki and Ferris, 2009) and inclines, the ankle muscle–tendon system delivers positive mechanical work with remarkably high 'apparent efficiency'. Future studies could use powered exoskeletons to study the mechanics and energetics of muscle–tendons crossing other joints (hip and knee) and during other locomotor tasks (i.e. running, hopping or accelerating). In addition, combining this approach with non-invasive *in vivo* techniques (e.g. ultrasound measurements) could help validate our suggestions regarding changes in underlying muscle–tendon mechanical function during walking under different locomotor conditions.

Our findings have important implications for engineering devices designed to reduce the metabolic cost of locomotion. Although it seems counterintuitive, our results suggest that powering the joints that generate the most mechanical power during locomotion may not lead to the largest reductions in metabolic cost. A better approach might be to target the joints with muscle–tendons that utilize the most metabolic energy per unit of mechanical work (i.e. joints with the least efficient muscle–tendons). Our findings suggest that powering proximal joints (e.g. hip) where muscle work rather than recycled tendon elastic energy contributes most of the muscle–tendon positive mechanical work may lead to the largest reductions in metabolic cost (Ferris et al., 2007). This would be especially true for walking uphill, where the hip muscle–tendons probably perform more of the total positive work than muscle–tendons crossing other joints and presumably with lower efficiency. A large workload at low efficiency would make the hip joint muscle–tendons relatively expensive, metabolically speaking.

LIST OF ABBREVIATIONS

EMG	electromyography
r.m.s.	root mean square
η^{+}_{ankle}	ankle MT 'apparent efficiency' of positive mechanical work
η^{+}_{muscle}	'muscular efficiency' of positive mechanical work

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REFERENCES

Asmussen, E. and Bonde-Petersen, F. (1974). Apparent efficiency and storage of elastic energy in human muscles during exercise. *Acta Physiol. Scand.* **92**, 537-545.
Bertram, J. E. and Ruina, A. (2001). Multiple walking speed-frequency relations are predicted by constrained optimization. *J. Theor. Biol.* **209**, 445-453.
Biewener, A. A. (1989). Scaling body support in mammals-limb posture and muscle mechanics. *Science* **245**, 45-48.
Biewener, A. A., Farley, C. T., Roberts, T. J. and Temaner, M. (2004a). Muscle mechanical advantage of human walking and running: implications for energy cost. *J. Appl. Physiol.* **97**, 2266-2274.
Biewener, A. A., McGowan, C., Card, G. M. and Baudinette, R. V. (2004b). Dynamics of leg muscle function in tammar wallabies (*M. eugenii*) during level *versus* incline hopping. *J. Exp. Biol.* **207**, 211-223.
Browning, R. C., Modica, J. R., Kram, R. and Goswami, A. (2007). The effects of adding mass to the legs on the energetics and biomechanics of walking. *Med. Sci. Sports Exerc.* **39**, 515-525.
Cavagna, G. A. and Kaneko, M. (1977). Mechanical work and efficiency in level walking and running. *J. Physiol. (Lond.)* **268**, 647-681.
Daley, M. A. and Biewener, A. A. (2003). Muscle force-length dynamics during level *versus* incline locomotion: a comparison of *in vivo* performance of two guinea fowl ankle extensors. *J. Exp. Biol.* **206**, 2941-2958.
Davies, C. T. and Barnes, C. (1972). Negative (eccentric) work. II. Physiological responses to walking uphill and downhill on a motor-driven treadmill. *Ergonomics* **15**, 121-131.
Doke, J. and Kuo, A. D. (2007). Energetic cost of producing cyclic muscle force, rather than work, to swing the human leg. *J. Exp. Biol.* **210**, 2390-2398.
Doke, J., Donelan, J. M. and Kuo, A. D. (2005). Mechanics and energetics of swinging the human leg. *J. Exp. Biol.* **208**, 439-445.
Donelan, J. M., Kram, R. and Kuo, A. D. (2001). Mechanical and metabolic determinants of the preferred step width in human walking. *Proc. R. Soc. Lond., B, Biol. Sci.* **268**, 1985-1992.
Donelan, J. M., Kram, R. and Kuo, A. D. (2002a). Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking. *J. Exp. Biol.* **205**, 3717-3727.
Donelan, J. M., Kram, R. and Kuo, A. D. (2002b). Simultaneous positive and negative external mechanical work in human walking. *J. Biomech.* **35**, 117-124.
Ferris, D. P., Czerniecki, J. M. and Hannaford, B. (2005). An ankle-foot orthosis powered by artificial pneumatic muscles. *J. Appl. Biomech.* **21**, 189-197.
Ferris, D. P., Gordon, K. E., Sawicki, G. S. and Peethambaran, A. (2006). An improved powered ankle-foot orthosis using proportional myoelectric control. *Gait Posture* **23**, 425-428.
Ferris, D. P., Sawicki, G. S. and Daley, M. A. (2007). A physiologist's perspective on robotic exoskeletons for human locomotion. *Int. J. Hum. Robot.* **4**, 507-528.
Fukunaga, T., Kubo, K., Kawakami, Y., Fukashiro, S., Kanehisa, H. and Maganaris, C. N. (2001). *In vivo* behaviour of human muscle tendon during walking. *Proc. R. Soc. Lond., B, Biol. Sci.* **268**, 229-233.
Gabaldon, A. M., Nelson, F. E. and Roberts, T. J. (2004). Mechanical function of two ankle extensors in wild turkeys: shifts from energy production to energy absorption during incline *versus* decline running. *J. Exp. Biol.* **207**, 2277-2288.
Gaesser, G. A. and Brooks, G. A. (1975). Muscular efficiency during steady-rate exercise: effects of speed and work rate. *J. Appl. Physiol.* **38**, 1132-1139.
Gordon, K. E. and Ferris, D. P. (2007). Learning to walk with a robotic ankle exoskeleton. *J. Biomech.* **40**, 2636-2644.
Gordon, K. E., Sawicki, G. S. and Ferris, D. P. (2006). Mechanical performance of artificial pneumatic muscles to power an ankle-foot orthosis. *J. Biomech.* **39**, 1832-1841.
Gottschall, J. S. and Kram, R. (2005). Energy cost and muscular activity required for leg swing during walking. *J. Appl. Physiol.* **99**, 23-30.
Grey, M. J., Nielsen, J. B., Mazzaro, N. and Sinkjaer, T. (2007). Positive force feedback in human walking. *J. Physiol.* **581**, 99-105.
Ishikawa, M., Komi, P. V., Grey, M. J., Lepola, V. and Bruggemann, G. P. (2005). Muscle–tendon interaction and elastic energy usage in human walking. *J. Appl. Physiol.* **99**, 603-608.
Kuo, A. D., Donelan, J. M. and Ruina, A. (2005). Energetic consequences of walking like an inverted pendulum: step-to-step transitions. *Exerc. Sport Sci. Rev.* **33**, 88-97.
Lay, A. N., Hass, C. J. and Gregor, R. J. (2006). The effects of sloped surfaces on locomotion: a kinematic and kinetic analysis. *J. Biomech.* **39**, 1621-1628.
Lay, A. N., Hass, C. J., Richard Nichols, T. and Gregor, R. J. (2007). The effects of sloped surfaces on locomotion: an electromyographic analysis. *J. Biomech.* **40**, 1276-1285.
Leroux, A., Fung, J. and Barbeau, H. (1999). Adaptation of the walking pattern to uphill walking in normal and spinal-cord injured subjects. *Exp. Brain Res.* **126**, 359-368.
Lewis, C., Kao, P. and Ferris, D. P. (2008). Invariant ankle joint moment patterns with plantar flexor assistance from a powered ankle orthosis. *North American Conference on Biomechanics, August 5-9, Ann Arbor, Michigan, USA*.
Lichtwark, G. A. and Wilson, A. M. (2006). Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. *J. Exp. Biol.* **209**, 4379-4388.
Margaria, R. (1938). Sulla fisiologia e specialmente sul consumo energetico della marcia e della corsa a varie velocita ed inclinazioni del terreno. *Atti Accad. Naz. Lincei Memorie, serie VI* **7**, 299-368.
Margaria, R. (1968). Positive and negative work performances and their efficiencies in human locomotion. *Int. Z. Angew. Physiol.* **25**, 339-351.
McGowan, C. P., Baudinette, R. V. and Biewener, A. A. (2007). Modulation of proximal muscle function during level versus incline hopping in tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **210**, 1255-1265.
McIntosh, A. S., Beatty, K. T., Dwan, L. N. and Vickers, D. R. (2006). Gait dynamics on an inclined walkway. *J. Biomech.* **39**, 2491-2502.
Minetti, A. E., Ardigo, L. P. and Saibene, F. (1993). Mechanical determinants of gradient walking energetics in man. *J. Physiol. (Lond.)* **472**, 725-735.
Roberts, T. J. and Belliveau, R. A. (2005). Sources of mechanical power for uphill running in humans. *J. Exp. Biol.* **208**, 1963-1970.
Roberts, T. J., Marsh, R. L., Weyand, P. G. and Taylor, C. R. (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113-1115.
Rubenson, J., Henry, H. T., Dimoulas, P. M. and Marsh, R. L. (2006). The cost of running uphill: linking organismal and muscle energy use in guinea fowl (*Numida meleagris*). *J. Exp. Biol.* **209**, 2395-2408.
Ryschon, T. W., Fowler, M. D., Wysong, R. E., Anthony, A. and Balaban, R. S. (1997). Efficiency of human skeletal muscle *in vivo*: comparison of isometric, concentric, and eccentric muscle action. *J. Appl. Physiol.* **83**, 867-874.
Sawicki, G. S. and Ferris, D. P. (2008). Mechanics and energetics of level walking with powered ankle exoskeletons. *J. Exp. Biol.* **211**, 1402-1413.
Sawicki, G. S. and Ferris, D. P. (2009). Powered ankle exoskeletons reveal the metabolic cost of plantar flexor mechanical work during walking with longer steps at constant step frequency. *J. Exp. Biol.* **212**, 21-31.
Sawicki, G. S., Gordon, K. E. and Ferris, D. P. (2005). Powered lower limb orthoses: applications in motor adaptation and rehabilitation. In *IEEE International Conference on Rehabilitation Robotics*. Chicago, IL: IEEE.
Smith, N. P., Barclay, C. J. and Loiselle, D. S. (2005). The efficiency of muscle contraction. *Prog. Biophys. Mol. Biol.* **88**, 1-58.
Whipp, B. J. and Wasserman, K. (1969). Efficiency of muscular work. *J. Appl. Physiol.* **26**, 644-648.