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RESEARCH ARTICLE

Biomechanical effects of augmented ankle power output during human walking

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ABSTRACT

The plantarflexor muscles are critical for forward propulsion and leg swing initiation during the push-off phase of walking, serving to modulate step length and walking speed. However, reduced ankle power output is common in aging and gait pathology, and is considered a root biomechanical cause of compensatory increases in hip power generation and increased metabolic energy cost. There is a critical need for mechanistic insight into the precise influence of ankle power output on patterns of mechanical power generation at the individual joint and limb levels during walking. We also posit that rehabilitative approaches to improve locomotor patterns should consider more direct means to elicit favorable changes in ankle power output. Thus, here we used real-time inverse dynamics in a visual biofeedback paradigm to test young adults' ability to modulate ankle power output during preferred speed treadmill walking, and the effects thereof on gait kinematics and kinetics. Subjects successfully modulated peak ankle power in response to biofeedback targets designed to elicit up to ±20% of normal walking values. Increasing ankle power output alleviated mechanical power demands at the hip and increased trailing limb positive work, propulsive ground reaction forces and step lengths. Decreasing ankle power had the opposite effects. We conclude that ankle power generation systematically influences the workload placed on more proximal leg muscles, trailing leg mechanical output and step length. Our findings also provide a promising benchmark for the application of biofeedback to restore ankle power in individuals with deficits thereof due to aging and gait pathology.

KEY WORDS: Joint work, Push-off, Walking, Metabolic cost, Inverse dynamics

INTRODUCTION

Extensor muscles spanning the ankle (i.e. plantarflexors) are a critical functional component of the human musculoskeletal system, powering daily activities such as walking. These muscles generate as much as 50% of the total mechanical power needed for vertical support, forward propulsion and leg swing initiation during the terminal stance phase, and are presumed critical for modulating step length and walking speed (Farris and Sawicki, 2012; Meinders et al., 1998; Neptune et al., 2009a, 2001). Moreover, the biological architecture of the plantarflexor muscles (i.e. short pennate fascicles and long tendons) is well suited for economical force and power generation during ankle push-off (Sawicki et al., 2009; Zelik et al., 2014). Accordingly, the well-documented and disproportionate effects of aging and many gait pathologies (e.g. stroke) on reducing ankle power output during walking are regularly accompanied by shorter steps, slower speeds and reduced walking economy (i.e. rate of oxygen consumption per unit distance) (DeVita and Hortobagyi, 2000; Farris et al., 2015; Franz, 2016; JudgeRoy et al., 1996; McGibbon et al., 2003; Winter et al., 1990). However, before we can implicate ankle power output in precipitating functional changes associated with aging and gait pathology, it is fundamentally important to understand its precise influence on joint- and limb-level biomechanics during normal walking in healthy young subjects.

Ankle power generation during the push-off phase of walking decreases by 11–35% in old age and can decrease by more than 50% in stroke survivors (Beijersbergen et al., 2017a; DeVita and Hortobagyi, 2000; Farris et al., 2015; Franz, 2016; JudgeRoy et al., 1996; McGibbon et al., 2003; Winter et al., 1990). In addition to the immediate functional implications, any reduction in ankle power output is also accompanied by increases in mechanical power demands from muscles spanning more proximal leg joints (Lewis and Ferris, 2008). Moreover, redistributing mechanical power demands to the hip could have implications for walking economy (Beijersbergen et al., 2017a; DeVita and Hortobagyi, 2000; JudgeRoy et al., 1996; McGibbon et al., 2003; Winter et al., 1990). Indeed, compensating for lack of ankle power output by redistributing lower limb mechanical workload to more proximal muscles has emerged as one potential explanation for reduced walking economy, both in old age and in people with gait pathology (Farris et al., 2015; Franz, 2016; Zelik et al., 2014). Some support for this notion comes from Huang et al. (2015), who restricted ankle joint rotation in young adults and found that, for every unit reduction in trailing limb power generation during push-off, hip and knee power generation during single support increased by an average of one unit and metabolic power by more than two units (Huang et al., 2015). However, the experimental paradigm used in that study placed the ankle, knee and hip joints in exaggerated flexion across the gait cycle and thus not only redistributed workload to more proximal leg muscles, but also increased the demand for total positive work overall. Thus, the extent to which requirements for mechanical power generation at the individual joint and limb levels, and in particular compensatory demands at the hip, are influenced by ankle power output during the push-off phase of walking remains uncertain.

The simplest explanation for reduced ankle power generation due to old age or gait pathology is that these changes emerge in people after succumbing to functional capacity limitations at the muscle level, for example via muscle weakness associated with sarcopenia (Baumgartner et al., 1998). Accordingly, conventional interventions, including muscle strengthening and power training, have garnered significant scientific attention and been the focus of clinical trials (Beijersbergen et al., 2013). The results from these

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Received 5 April 2018; Accepted 21 September 2018

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Journal of Experimental Biology (2018) 221, jeb182113. doi:10.1242/jeb.182113

studies are equivocal, and muscle strength gains are, by design, almost unanimously reported. However, a relatively recent and rigorous power training study in older adults, designed to enhance ankle power generation during walking, conveyed benefits only during maximum speed walking (Beijersbergen et al., 2017b). The cumulative insights from these studies suggest that improving maximum muscular capacity may fail to alter the instinctive utilization of that capacity during gait, thereby conveying little functional improvement for normal, habitual-speed walking. Indeed, we and others have revealed evidence that many individuals, even after succumbing to deficits in ankle power output, actually underutilize their available capacity for generating forward propulsion during walking. The availability of these 'propulsive reserves', now evident in older adults (Franz, 2016) and stroke survivors (Wang et al., 2015), challenges our understanding of ankle power output in walking and its role in shaping walking performance and walking economy. Moreover, rehabilitative approaches that go beyond resistance training alone may have the potential to more directly elicit favorable biomechanical adaptations during habitual-speed walking.

Real-time biofeedback has a long and successful history as a paradigm to gain fundamental insight into the biomechanics of locomotion (Browne and Franz, 2017) and to facilitate a return to normal locomotor function following stroke (Binder et al., 1981; Colborne et al., 1993; Intiso et al., 1994), amputation (Isakov, 2007) or total joint replacement (Isakov, 2007; White and Lifeso, 2005), for example. However, knowing the appropriate biomechanical outcome to target in these paradigms is paramount to their scientific impact and translational success. For example, we have shown that visual biofeedback targeting propulsive deficits in older adults, through real-time ground reaction force (GRF) measurements during treadmill walking, can elicit peak propulsive forces that are equal to or even larger than those of young adults walking at the same speed (Franz et al., 2014). Genthe et al. (2018) used a similar biofeedback approach in a unilateral paradigm designed to enhance push-off intensity in people with post-stroke hemiparesis. We had presumed that, in human walking, people would respond to propulsive force biofeedback through increases in ankle moment and thus ankle power generation that mirrored those in propulsive forces. However, we were more recently surprised to discover that, independent of age, people opt to increase propulsive forces without augmenting ankle moment or power output (Browne and Franz, 2018). Those results imply a need to more fully understand the influence of ankle joint kinetics on the biomechanics in human walking while also pointing to translational opportunities for real-time biofeedback that more directly targets improvements in ankle power generation.

Therefore, as an important first step, our purpose was to investigate the effects of real-time peak ankle power biofeedback on gait kinematics and kinetics during walking in young adults. For this study, we used targeted visual biofeedback based on real-time inverse dynamics to test young adults' ability to effectively modulate their ankle power from one step to the next. At a more fundamental level, this study sought to gain mechanistic insight into the role of ankle power output in modulating patterns of mechanical power generation across the lower limb joints during walking. We first hypothesized that young adults have the capacity to volitionally modulate ankle power via biofeedback when walking at their preferred speed. Second, we hypothesized that increased/decreased ankle power output during push-off at each subject's preferred speed would decrease/increase the mechanical workload placed on muscles spanning the hip. Finally, we hypothesized that ankle power output, accompanied by those offsetting biomechanical changes at the hip, would alter the distribution of power generation across the leg joints without affecting total positive joint work.

MATERIALS AND METHODS

Subjects

Ten healthy young adults (5 males/5 females, means±s.d.; age: 24.8±5.4 years, mass: 73.2±7.6 kg, height: 1.78±0.09 m) participated in this study. All subjects were free of neurological impairments and musculoskeletal injury, and walked in their own athletic footwear during the study. Subjects participated after providing written, informed consent according to the University of North Carolina Chapel Hill Biomedical Sciences Institutional Review Board.

Visual biofeedback

This experiment utilized a novel visual biofeedback paradigm based on real-time inverse dynamics using force measurements from a dual-belt instrumented treadmill (Bertec, Corp., Columbus, OH, USA) and a 14-camera motion capture system (Motion Analysis Corporation, Santa Rosa, CA, USA). Specifically, for trials involving biofeedback, a custom MatLab (MathWorks, Natick, MA, USA) script continuously estimated the average bilateral peak ankle power during push-off from each set of four consecutive steps and projected a visual representation of those values as dots in real time to a screen positioned in front of the treadmill. After detecting heel-strike using a 20 N vertical GRF threshold, assuming a massless foot, the script developed a simplified bilateral inverse dynamics model of the shank and foot segments for moment and angular velocity estimations. While the foot was on the ground, we constructed vector representations in each frame of the shank (lateral malleoli to the average lateral shank cluster position) and the foot (lateral malleoli to fifth metatarsal–phalangeal joint). Also in each frame, we estimated a 3-dimensional position vector (r_{A}) between the instantaneous lateral malleoli marker position and the center of pressure location. The script then estimated the instantaneous ankle moment ($M_{\mathrm{A}}^{\mathrm{RT}}$) by taking the cross product of the 3-dimensional moment arm and the 3-axis GRF vectors per Eqn 1:

$$(M_{\mathrm{A},x}^{\mathrm{RT}} \;\; M_{\mathrm{A},y}^{\mathrm{RT}} \;\; M_{\mathrm{A},z}^{\mathrm{RT}}) = (r_{\mathrm{A},x} \;\; r_{\mathrm{A},y} \;\; r_{\mathrm{A},z}) \times (F_x \;\; F_y \;\; F_z). \quad (1)$$

Here, x, y and z correspond to the mediolateral, anterior–posterior and vertical directions in the global coordinate system, respectively. Using the same segmental definitions, we estimated the sagittal plane ankle angular velocity ($\omega_{\mathrm{A}}^{\mathrm{RT}}$) across the entire stance phase directly from vectors formed from the shank cluster, lateral malleoli and fifth metatarsal–phalangeal joint. Finally, we estimated real-time ankle power ($P_{\mathrm{A}}^{\mathrm{RT}}$) during stance as per Eqn 2:

$$P_{\mathrm{A}}^{\mathrm{RT}} = M_{\mathrm{A},x}^{\mathrm{RT}} \cdot \omega_{\mathrm{A}}^{\mathrm{RT}}. \quad (2)$$

Peak $P_{\mathrm{A}}^{\mathrm{RT}}$ was extracted bilaterally from each step, and a 4-step moving average was projected as a dot on a screen in the front of the treadmill, thereby serving as step-by-step biofeedback. We then encouraged subjects to match their step-by-step $P_{\mathrm{A}}^{\mathrm{RT}}$ to target values displayed as horizontal lines, prescribed according to the experiment outlined below. For all trials involving visual biofeedback, we normalized the scaling of each subject's feedback data on the projected display to evenly distribute all target values over the ordinate range.

Experimental protocol

A photo cell timing system assessed the subjects' preferred overground walking speed as the average of 3 times taken to

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traverse the middle 2 m of a 10 m walkway (Bower Timing Systems, Draper, UT, USA). Subjects then completed all walking trials on the instrumented treadmill (Bertec, Columbus, OH, USA) at their preferred speed (i.e. 1.27±0.14 m s^{-1}). First, subjects walked normally for 90 s while our MatLab routines monitored their instantaneous ankle power. We immediately used those data to estimate each subjects' habitual P_A^{RT} for use in subsequent visual biofeedback trials. Prior to biofeedback trials, each subject completed a 3 min exploration period without targets to accommodate to and practice using P_A^{RT} biofeedback. We also explained the concept of ankle power to each subject, including its timing and brief descriptions of ankle moment and angular velocity. Then, during a 90 s trials, subjects modified their instantaneous ankle power to match target values representing ±10% and ±20% of habitual ankle power in a fully randomized order.

Measurement and analysis

A 14-camera motion capture system (Motion Analysis Corporation) operating at 100 Hz recorded pelvis and lower extremity kinematics via 17 anatomical markers and an additional 14 tracking markers affixed using rigid clusters. Analog GRF data were recorded at 1000 Hz. A standing calibration trial also included medial knee and ankle joint anatomical markers.

Marker trajectories and GRF data were filtered using fourth-order low-pass Butterworth filters with cutoff frequencies of 6 and 100 Hz, respectively. We then used the static standing calibration and functional hip joint centers from a leg circumduction task (Piazza et al., 2001) to scale a 7 segment, 18 degrees-of-freedom model of the pelvis and right and left legs (Arnold et al., 2010). We used the filtered marker and GRF data to estimate hip, knee and ankle joint angles, moments and powers (e.g. ankle power: P_A) using an inverse dynamics routine described in detail previously (Silder et al., 2008). Also at the joint level, positive hip, knee and ankle joint work were calculated as the positive area under the respective joint power curve. In addition, to gain insight into how individual joint mechanics altered center of mass (CoM) mechanics, we used the individual limbs method (Donelan et al., 2002) and measured GRF data to estimate positive and negative mechanical work performed on the CoM by the leading and trailing legs during double support and the stance leg during single support. For example, power generated at the ankle can be offset via changes in power absorption at other joints (Toney and Chang, 2016), motivating our inclusion of this limb-level analysis. Specifically, we derived the CoM power curves as the dot product of CoM velocity and the sum of the individual limbs GRF using previously published procedures (Donelan et al., 2002) and integrated those curves with respect to time. For each subject, we selected for analysis the 20 consecutive strides from each 90 s trial averaging nearest to each associated target value (i.e. ±10% and ±20%).

Statistical analysis

Shapiro–Wilks tests confirmed normal distributions for each outcome measure (i.e. P_A^{RT}, P_A, hip, knee and ankle joint angles, moments and powers, CoM work). We used paired *t*-tests to assess differences between P_A^{RT} and P_A. Those tests also assessed the symmetry of the subjects' response to biofeedback by comparing the change in peak ankle power from normal walking to each biofeedback target between their right and left legs. We then tested for main effects of P_A^{RT} biofeedback on all outcome measures using one-way repeated measures analyses of variance (ANOVA) and an alpha level of 0.05. When a significant main effect was found, planned *post hoc* pairwise comparisons were focused between normal walking and walking with the 4 modulated ankle power targets. To provide context, we report effect sizes for all ANOVA results [i.e. partial eta squared (η_P^2)].

RESULTS

Ankle power and biofeedback efficacy

Our real-time surrogate for peak ankle power systematically overestimated full inverse dynamics estimates by only 5% across all conditions (P<0.001) (Fig. 1). Nevertheless, a significant main effect revealed that subjects successfully modulated peak ankle power ($P_A^{RT}$and P_A) in response to biofeedback as intended (P<0.001, η_P^2 >0.810), a response that did not differ between their right and left legs (P≥0.0127). Pairwise comparisons showed that subjects, on average, increased P_A by 10±11% (P=0.013) and 13±11% (P=0.003) in response to +10% and +20% targets, respectively, and decreased P_A by 13±12% (P=0.001) and 28±16% (P<0.001) in response to −10% and −20% targets, respectively.

Ankle and hip joint kinetics and kinematics

Increasing/decreasing peak ankle power during push-off decreased/increased peak hip joint power output on the ipsilateral limb during terminal stance and early swing (main effect, P=0.038, η_P^2=0.240) and on the contralateral limb during early to mid-stance (main effect, P<0.001, η_P^2=0.450) (Fig. 2). For example, on the ipsilateral limb, a target 20% increase in peak ankle power decreased peak hip flexor power generation from 1.54±0.42 to 1.16±0.52 W kg^{-1} (i.e. −25%, P=0.032). Simultaneously, this same condition also tended to decrease contralateral limb hip extensor power generation from 0.91±0.40 to 0.66±0.30 W kg^{-1} (i.e. −28%, P=0.072). We also found a main effect of modulating peak ankle power on peak ankle moment (P<0.001, η_P^2=0.521), although pairwise comparisons revealed that this was driven only by targeting reductions in ankle power (P≤0.010; Fig. 2). Indeed, target increases in peak ankle power were more associated with increased peak ankle angular velocity (main effect, P<0.001, η_P^2=0.659), for example increasing from 368±88 to 441±81 deg s^{-1} for +10% target values (P=0.003). Increasing peak ankle power also significantly increased peak ankle extension, while decreasing ankle power significantly decreased both peak ankle and peak hip extension (main effects, ankle: P<0.001, η_P^2=0.772; hip: P=0.045, η_P^2=0.231) (Fig. 2). Lastly, we found a main effect of condition on step length, with changes mirroring those in ankle power output across the range of target values (P=0.012, η_P^2=0.294).

Joint work, CoM work and propulsive forces

Modulating peak ankle power output altered the distribution of positive mechanical work performed about the individual leg joints and also systematically affected total (hip+knee+ankle) positive joint work (Fig. 3A). First, compared with normal walking, a target 20% increase/decrease in peak ankle power elicited a 32±24% increase (23±17% decrease) in positive ankle joint work (main effect, P<0.001, η_P^2=0.767; pairwise, P≤0.015). Changes in ankle joint work were accompanied by opposing changes in total positive hip joint work (main effect, P<0.001, η_P^2=0.437); for example, a target 20% increase in peak ankle power tended to decrease positive hip joint work from 0.27±0.06 to 0.21±0.08 J kg^{-1} (i.e. −20%, P=0.062). These opposing changes in positive mechanical work at the ankle and hip, with no effects at the knee, yielded relatively invariant total positive leg joint work when targeting larger than preferred peak ankle power. In contrast, a significant main effect of modulating peak ankle power on total positive joint work (P<0.001,

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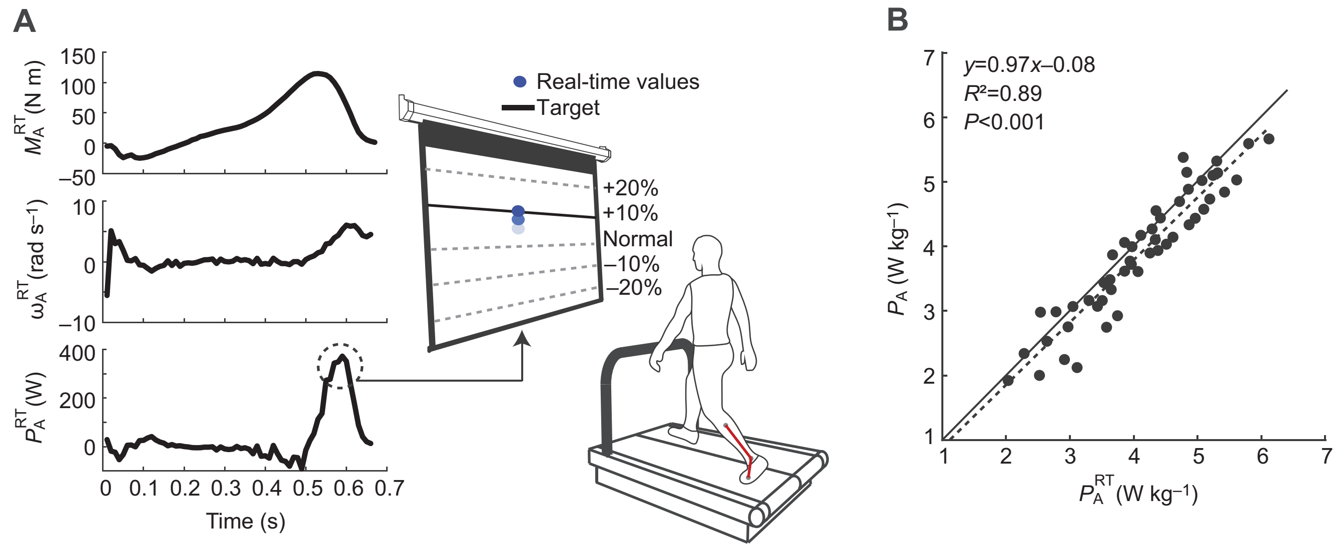

Fig. 1. Real-time inverse dynamics and ankle power biofeedback paradigm. (A) We implemented a surrogate inverse dynamics model of the lower leg and foot to estimate, in real-time (RT), the instantaneous ankle moment (M_A^{RT}) and angular velocity (ω_A^{RT}), which we then used to estimate step-by-step peak ankle power (P_A^{RT}). Representative raw data from a single stance phase is shown. Step-by-step peak ankle power was projected onto a screen positioned in front of the treadmill along with, in different trials, target lines representing ±10% and ±20% of normal. (B) Linear regression between real-time surrogate peak ankle power (P_A^{RT})and actual post-processed peak ankle power (P_A), pooled across all subjects (n=10) and conditions, showed good agreement. Each data point represents the stride-averaged data for one condition for one subject. The dashed line represents the line of best fit, and the solid line represents the line of unity.

η_P^2=0.530) was driven by disproportionate decreases in positive ankle joint work and thus total joint work for target 10% (P=0.013) and 20% (P=0.006) decreases in peak ankle power .

These changes in joint work also altered CoM mechanics during double support; we found a significant main effect of modulating peak ankle power on CoM work (Fig. 3B) performed by the trailing limb (positive work: P<0.001, η_P^2=0.620) and leading limb (negative work: P=0.007, η_P^2=0.320). During double support, modulating peak ankle power elicited pairwise differences in positive trailing limb CoM work compared with normal walking; for example, increasing from 0.22±0.04 to 0.26±0.06 J kg^{-1} (i.e. +20% target, P=0.044) and decreasing to 0.15±0.05 J kg^{-1} (i.e. −20% target, P=0.002). Conversely, only increases in peak ankle power elicited pairwise differences in leading limb negative CoM work during double support compared to normal walking, with leading limb negative CoM increasing from −0.16±0.05 to up to

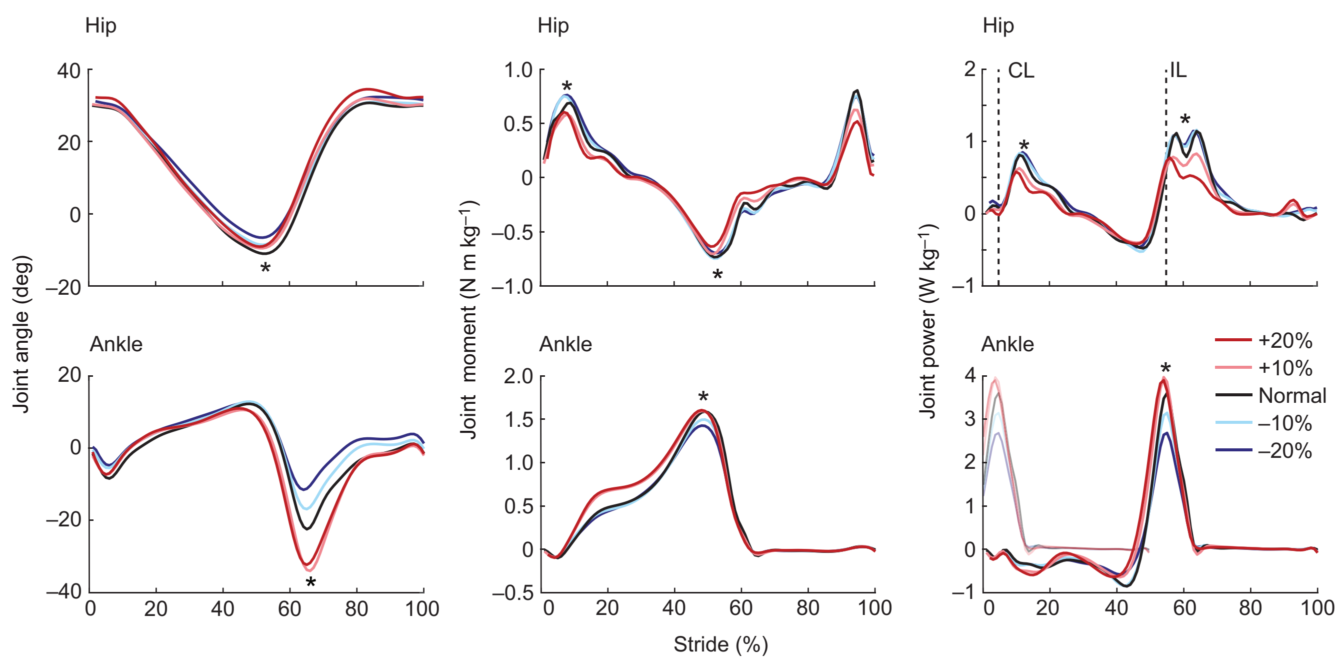

Fig. 2. Group mean (n=10) hip and ankle joint angles, moments and powers plotted against an average stride during normal walking and when modulating peak ankle power in response to biofeedback. Asterisks indicate local maxima or minima exhibiting a significant ANOVA main effect of modulating peak ankle power via biofeedback (P<0.05). Positive values indicate joint flexion, internal extensor moments and power generation, respectively. Vertical dashed lines on the hip joint power curves indicate the timing of peak ankle power generated via the contralateral (CL) and ipsilateral (IL) limbs.

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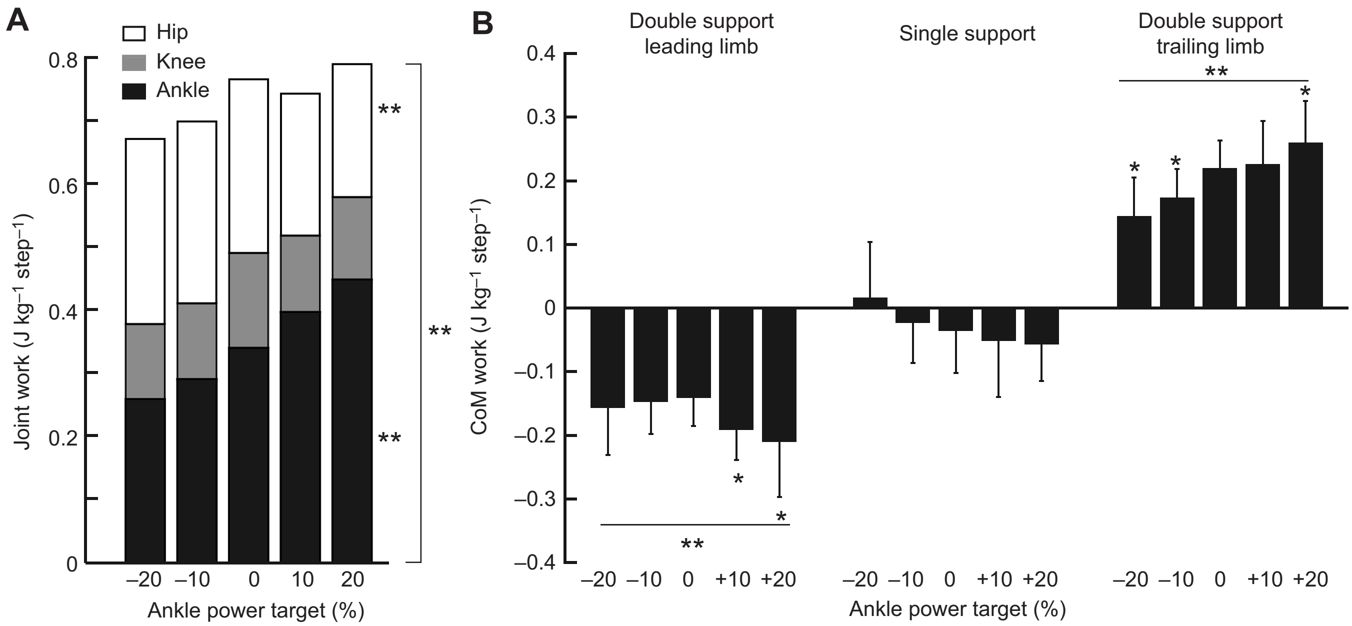

Fig. 3. Group mean (n=10) leg joint and center of mass (CoM) mechanical work during normal walking and when modulating peak ankle power in response to biofeedback. (A) Group mean total positive hip, knee and ankle joint work per step across all conditions, calculated as the time integral of the respective joint power curve. Double asterisks indicate a significant ANOVA main effect of modulating peak ankle power via biofeedback on positive ankle joint work and total positive joint work (i.e. the sum of the hip, knee and ankle) (P<0.05). (B) Group mean (±s.d.) net mechanical work per step performed on the CoM by the leading and trailing limb during double support and by the stance limb during single support across all conditions. Double asterisks indicate a significant main effect of modulating peak ankle power via biofeedback on double support CoM mechanics (P<0.05). Single asterisks indicate significant pairwise comparisons versus normal walking (P<0.05). Here, with treadmill speed fixed, total net work performed on the CoM is zero. Accordingly, increases in positive trailing leg work (when targeting larger than preferred peak ankle power) were accompanied by increases in leading leg negative work. Conversely, decreases in trailing leg work (when targeting smaller than preferred peak ankle power) were accompanied by a subtle (and non-significant) shift toward net positive work during single support.

−0.25±0.13 J kg^{-1} (i.e. +60%, P=0.030). Finally, we found changes in peak anterior–posterior GRFs that mirrored those in peak ankle power (e.g. peak propulsive: P<0.001, η^2_P=0.688; Fig. 4). For example, a target 20% increase/decrease in peak ankle power increased/decreased peak propulsive force from 20.5±3.0 to 25.3± 4.8%BW (17.5±3.4%BW), respectively (P≤0.003).

DISCUSSION

Many individuals experience a reduction in peak ankle power during the push-off phase of walking, independent of walking speed, as they succumb to the effects of aging or gait pathology (Farris et al., 2015; Franz, 2016). This deficit in mechanical power generation is considered by many to be a root cause, at least biomechanically, of functional limitations that include shorter steps, slower speeds and reduced walking economy. To our knowledge, the paradigm presented in this study as a proof of concept in young adults is the first to date to target that root cause, peak ankle power, via real-time biofeedback as a direct means to elicit favorable biomechanical adaptations during walking. Consistent with our first hypothesis, young adults had the ability to volitionally modulate

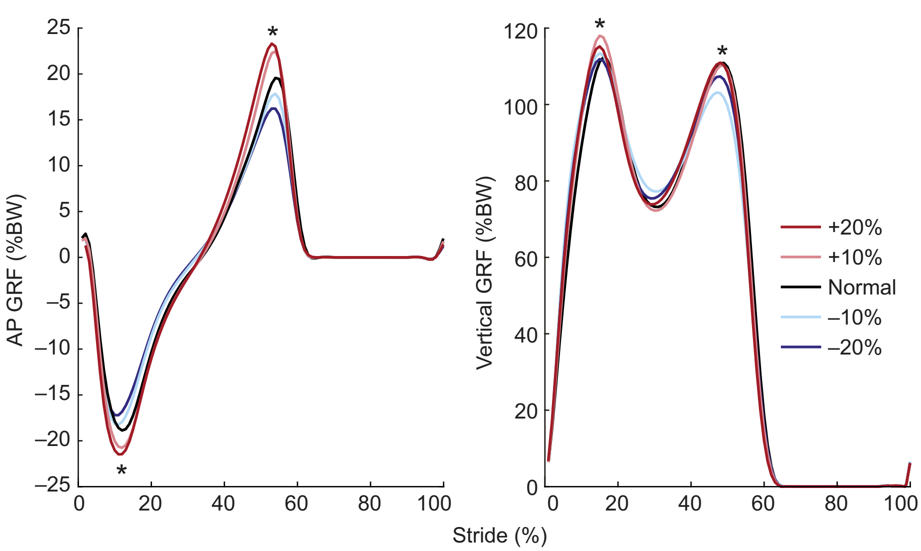

Fig. 4. Group mean (n=10) anterior–posterior (AP) and vertical ground reaction forces (GRF) plotted against an averaged stride during normal walking and when modulating peak ankle power in response to biofeedback. Asterisks indicate local maxima exhibiting a significant ANOVA main effect of modulating peak ankle power via biofeedback (P<0.05).

peak ankle power via biofeedback to prescribed target values in real time when walking at a constant speed. In addition, those changes in peak ankle power during push-off systematically affected mechanical power demands of muscles spanning the hip in a manner consistent with our second hypothesis. Specifically, we add here that increased/decreased ankle power output simultaneously decreased/increased mechanical power demands on the ipsilateral hip flexors and contralateral hip extensor muscles during and immediately following push-off. Finally, in partial support of our third hypothesis, due to proportional and offsetting biomechanical changes at the hip, total positive joint work was relatively insensitive to increases, but not decreases, in peak ankle power. Taken together, we provide empirical data demonstrating that ankle power output has an important influence on workload placed on more proximal leg muscles, propulsive GRFs and step lengths. Moreover, as we elaborate below, these data provide an important and promising benchmark for the application of biofeedback to restore ankle power in individuals with deficits thereof due to aging and gait pathology.

We first hypothesized that young adults could volitionally modulate peak ankle power via biofeedback. It may not be altogether surprising that our data fully supported this hypothesis, particularly in young healthy subjects. Nevertheless, we consider this outcome a meaningful contribution given the novelty of our biofeedback paradigm. We also note that our simplified surrogate model for estimating peak ankle power in real time, despite neglecting inertial effects and more sophisticated estimates of ankle joint center, very closely approximated peak ankle power derived from the full inverse dynamics model for all conditions. Moreover, the prescribed targets for modulating peak ankle power in this study represent those that we would consider functionally meaningful. For example, older adults generate 11–35% less ankle power than young adults walking at the same speed (Franz, 2016). For additional functional context, the regressions of Lelas et al. (2003) imply that a 20% increase in peak ankle power during walking, if performed over ground, would be associated with a 19% increase in walking speed compared to that freely selected by our subjects (i.e. 1.27–1.51 m s^{-1}) (Lelas et al., 2003). Here, we found that subjects were least successful, on average, at generating 20% greater than normal peak ankle power during push-off, averaging only +13%. It is possible that a 20% increase in peak ankle power is unachievable when walking at a constant speed. However, because we did not test larger percent changes, our results may not necessarily suggest that subjects had reached their maximum capacity for generating ankle power, and future studies should consider the efficacy of subjects' responses to more challenging target values. We also note that subjects volitionally increased peak ankle power more by changing ankle angular velocity during push-off than by changing peak ankle moment. Accordingly, the biological effects of decreased muscle force-generating capacity and decreased muscle shortening velocity, for example due to aging, may be equally relevant in understanding age-related changes in ankle power generation and response to similar biofeedback paradigms.

Our findings contribute to growing evidence implicating reduced ankle power output as a mechanism governing unfavorable increases in mechanical power demands from muscles spanning more proximal leg joints during walking, evident with aging and gait pathology (Browne and Franz, 2017; Farris et al., 2015; Franz, 2016; Huang et al., 2015). Indeed, consistent with our second hypothesis, we observed a clear tradeoff in mechanical workload between the ankle extensors during push-off and, simultaneously, the ipsilateral hip flexors during terminal stance and early swing, and the contralateral hip extensors during early to midstance. In bipedal locomotion, these events are nearly coincident. For example, right leg ankle extensor power generation coincides with right leg hip flexor power generation and immediately precedes left leg hip extensor power generation in order to redirect and accelerate the body's CoM with each step. Given a prerequisite mechanical power demand from the legs for walking (Farris and Sawicki, 2012), any reduction in ankle power output should necessitate a redistribution of mechanical power demands to some combination of flexor and extensor muscles spanning the hip – an expectation fully consistent with the subjects' response to biofeedback. Huang et al. (2015) recently found convincing evidence for a similar redistribution of mechanical workload to the hip using steel cables to restrict the ankle's ability to rotate into plantarflexion (Huang et al., 2015). However, while effective at reducing ankle power output during push-off, the physical constraint imposed on ankle joint rotation in that study positioned the ankle, knee and hip joints in exaggerated flexion throughout the gait cycle. In contrast, subjects' bilateral responses to targeted ankle power biofeedback was volitional, relatively isolated in timing to the push-off phase of walking, and yet still exemplified a characteristic distal–proximal tradeoff in mechanical power generation.

We posit that the data in support of our second hypothesis are functionally meaningful in the context of the biological architecture of muscle–tendon units spanning the leg joints, the relative metabolic costs associated with operating those muscle–tendon units and thus, ultimately, walking economy. Individuals that have succumbed to reductions in ankle power output during walking also exhibit reductions in walking economy. For example, older adults consume oxygen 15–20% faster than young adults walking at the same speed (Mian et al., 2006; Ortega and Farley, 2007). Although those changes are likely complex and multifactorial, compensating for lack of ankle power output by redistributing lower limb mechanical workload to more proximal muscles may be a contributing factor. Indeed, proximal muscle–tendon architecture, with their long fascicles and short tendons, may be less favorable for economically powering push-off than that of distal muscle–tendons that benefit from relatively shorter fascicles attached to long energy storing tendons (Sawicki et al., 2009; Zelik et al., 2014). Based on available evidence, it is not entirely clear whether substituting hip power output for ankle power output, due to the relative metabolic costs associated with operating muscle–tendon units spanning those joints, comes at a metabolic penalty. Redistributing mechanical workload to more proximal leg muscles in Huang et al. (2015) was accompanied by up to a 2-fold increase in metabolic energy cost of walking (Huang et al., 2015). Similarly, Zelik et al. (2014) used simulations to suggest that the metabolic costs of walking were lower when powered via ankle push-off rather than via the hip musculature. However, those increases in metabolic costs can also be explained by a simultaneous increase in the requirement for total positive mechanical work in both studies. Ultimately, our young adult subjects likely walked normally with a pattern of mechanical power generation that optimized metabolic energy cost (Selinger et al., 2015), such that increasing ankle power via biofeedback above normative levels likely costs more, metabolically. However, we posit that, in individuals with insufficient ankle power output, a similar biofeedback paradigm could have favorable effects not only on normalizing patterns of joint power generation, but thereby also on metabolic cost of walking – a major effort of our work moving forward.

Data only partially supported our third hypothesis. Several prior studies have found that the relative contributions from the ankle, knee and hip to total positive joint work are relatively well preserved across a wide range of walking speeds (Browne and Franz, 2017; Farris and Sawicki, 2012). In contrast, when walking at a constant speed, we find that increasing peak ankle power during push-off elicited proportional and offsetting changes between positive ankle and hip joint work – effects that served to preserve total positive joint work as hypothesized. Accordingly, one interesting and novel contribution of this study is that increases in ankle power output during the push-off phase of walking need not be associated with an increase in total positive joint work. Conversely, subjects disproportionately decreased ankle work and thus total positive joint work when walking with smaller than preferred peak ankle power. This outcome clearly demonstrates the sensitivity of leg joint power generation in walking to deficits in ankle power output. We also note that, despite offsetting biomechanical changes at the hip, modulating ankle power at the joint level did have influences at the limb level, systematically influencing peak propulsive GRFs and work performed on the body's CoM by the leading and trailing legs during double support.

There are two interesting implications of these findings. First, positive and negative work performed by the trailing and leading legs during double support, respectively, is tuned in magnitude and timing to efficiently and effectively redirect and accelerate the body's CoM to transition between one step and the next, at least in healthy young adults (Donelan et al., 2002; Zelik et al., 2014). This tuned, inter-dependent behavior in young adults was exemplified here: trailing leg positive work appeared most sensitive to less than normal ankle power, whereas leading leg negative work was most sensitive to greater than normal ankle power. Conversely, older adults and people with gait pathology not only exhibit deficits in push-off intensity at the joint level (i.e. ankle power output), but also at the limb level via diminished peak propulsive forces and trailing limb positive CoM work (Franz and Kram, 2013). Our results suggest that the benefits of ankle power biofeedback in people with reduced push-off intensity could thereby enhance forward propulsion at the whole-body level. Second, we were surprised to find previously that, when permitted with redundancy among the leg joints to generate larger peak propulsive forces via biofeedback, neither young nor older adults did so by increasing peak ankle power output during push-off (Browne and Franz, 2018). Thus, although increasing ankle power output is not a prerequisite for walking with larger than preferred propulsive forces, we add here that increasing ankle power output does lead to walking with larger propulsive force during push-off. This latter finding improves our fundamental understanding of the complex interplay between power generation at the joint level and propulsive force generation at the limb level.

We acknowledge several limitations in this study. As our primary purpose and hypotheses focused on lower limb and CoM mechanics, we did not record upper body kinematics, which may have varied with the biofeedback and influenced our outcome measures. We also studied healthy young subjects as a benchmark for the application of biofeedback to restore ankle power in individuals with deficits thereof due to aging and gait pathology. We cannot exclude the possibility that the biomechanical response to ankle power biofeedback could differ substantially in those more translationally relevant populations. Nevertheless, we also see this study as a novel contribution serving to improve our fundamental biomechanical understanding of the influence of ankle power on the biomechanics of walking. Toward this fundamental understanding, we opted to include and report external mechanical work performed on the body's CoM by forces exerted by the individual legs during walking as a complement to joint-level measures derived using inverse dynamics. Indeed, as one example, power generated at the ankle can be offset via changes in power absorption at other joints (Toney and Chang, 2016), motivating the need for limb-level analysis. However, we acknowledge that some authors (Neptune et al., 2004) have questioned the utility of those outcome measures to provide direct insight into muscle function and factors that affect walking economy and that this remains debated (Kuo and Donelan, 2009; Neptune et al., 2009b). Finally, although highly innovative, real-time inverse dynamics relies on having access to sophisticated measurement equipment that could obstruct its clinical adoption. However, with the advent of wearable and low-cost inertial measurement units, we envision the possibility to overcome these practical limitations.

In conclusion, our findings here in young adults provide mechanistic insight into the important influence that ankle power output during push-off has on workload placed on more proximal leg muscles, on trailing leg mechanical output and on step length. This study also introduces a visual biofeedback paradigm based on real-time inverse dynamics to target reductions in peak ankle power during walking commonly attributed to aging and gait pathology. Here, we establish a promising benchmark for the application of targeted biofeedback to restore ankle power in individuals with deficits thereof due to aging and gait pathology. Our translational hypothesis moving forward is that restoring peak ankle power output in people with deficits in push-off intensity could have favorable affects that include attenuating compensatory mechanical power demands on proximal leg muscles and normalizing metabolic energy cost of walking.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: M.G.B., J.R.F.; Methodology: M.G.B., J.R.F.; Validation: M.G.B., J.R.F.; Formal analysis: S.N.F., M.G.B., J.R.F.; Investigation: S.N.F., M.G.B., J.R.F.; Data curation: S.N.F., M.G.B., J.R.F.; Writing - original draft: S.N.F.; Writing - review & editing: S.N.F., M.G.B., J.R.F.; Visualization: S.N.F., M.G.B., J.R.F.; Supervision: J.R.F.; Project administration: J.R.F.; Funding acquisition: J.R.F.

Funding
This study was supported by a North Carolina State University Abrams Scholarship awarded to S.N.F. and by a grant from the National Institutes of Health (R01AG051748). Deposited in PMC for release after 12 months.

References
Arnold, E. M., Ward, S. R., Lieber, R. L. and Delp, S. L. (2010). A model of the lower limb for analysis of human movement. *Ann. Biomed. Eng.* **38**, 269-279.
Baumgartner, R. N., Koehler, K. M., Gallagher, D., Romero, L., Heymsfield, S. B., Ross, R. R., Garry, P. J. and Lindeman, R. D. (1998). Epidemiology of sarcopenia among the elderly in New Mexico. *Am. J. Epidemiol.* **147**, 755-763.
Beijersbergen, C. M. I., Granacher, U., Vandervoort, A. A., DeVita, P. and Hortobágyi, T. (2013). The biomechanical mechanism of how strength and power training improves walking speed in old adults remains unknown. *Ageing Res. Rev.* **12**, 618-627.
Beijersbergen, C. M. I., Granacher, U., Gäbler, M., DeVita, P. and Hortobágyi, T. (2017a). Hip mechanics underlie lower extremity power training-induced increase in old adults' fast gait velocity: the Potsdam Gait Study (POGS). *Gait Posture* **52**, 338-344.
Beijersbergen, C. M. I., Granacher, U., Gäbler, M., DeVita, P. and Hortobágyi, T. (2017b). Kinematic mechanisms of how power training improves healthy old adults' gait velocity. *Med. Sci. Sports Exerc.* **49**, 150-157.
Binder, S. A., Moll, C. B. and Wolf, S. L. (1981). Evaluation of electromyographic biofeedback as an adjunct to therapeutic exercise in treating the lower extremities of hemiplegic patients. *Phys. Ther.* **61**, 886-893.
Browne, M. G. and Franz, J. R. (2017). The independent effects of speed and propulsive force on joint power generation in walking. *J. Biomech.* **55**, 48-55.
Browne, M. and Franz, J. R. (2018). More push from your push-off: joint-level modifications to modulate propulsive forces in old age. *PLoS ONE* **13**, e0201407.

Colborne, G. R., Olney, S. J. and Griffin, M. P. (1993). Feedback of ankle joint angle and soleus electromyography in the rehabilitation of hemiplegic gait. *Arch. Phys. Med. Rehabil.* **74**, 1100-1106.

DeVita, P. and Hortobagyi, T. (2000). Age causes a redistribution of joint torques and powers during gait. *J. Appl. Physiol.* **88**, 1804-1811.

Donelan, J. M., Kram, R. and Kuo, A. D. (2002). Simultaneous positive and negative external mechanical work in human walking. *J. Biomech.* **35**, 117-124.

Farris, D. J. and Sawicki, G. S. (2012). The mechanics and energetics of human walking and running: a joint level perspective. *J. R Soc. Interface* **9**, 110-118.

Farris, D. J., Hampton, A., Lewek, M. D. and Sawicki, G. S. (2015). Revisiting the mechanics and energetics of walking in individuals with chronic hemiparesis following stroke: from individual limbs to lower limb joints. *J. Neuroeng. Rehabil.* **12**, 24.

Franz, J. R. (2016). The age-associated reduction in propulsive power generation in walking. *Exerc. Sport Sci. Rev.* **44**, 129-136.

Franz, J. R. and Kram, R. (2013). Advanced age affects the individual leg mechanics of level, uphill, and downhill walking. *J. Biomech.* **46**, 535-540.

Franz, J. R., Maletis, M. and Kram, R. (2014). Real-time feedback enhances forward propulsion during walking in old adults. *Clin. Biomech.* **29**, 68-74.

Genthe, K., Schenck, C., Eicholtz, S., Zajac-Cox, L., Wolf, S. and Kesar, T. M. (2018). Effects of real-time gait biofeedback on paretic propulsion and gait biomechanics in individuals post-stroke. *Top. Stroke Rehabil.* **25**, 186-193.

Huang, T.-P., Shorter, K. A., Adamczyk, P. G. and Kuo, A. D. (2015). Mechanical and energetic consequences of reduced ankle plantarflexion in human walking. *J. Exp. Biol.* **218**, 3541-3550.

Intiso, D., Santilli, V., Grasso, M. G., Rossi, R. and Caruso, I. (1994). Rehabilitation of walking with electromyographic biofeedback in foot-drop after stroke. *Stroke* **25**, 1189-1192.

Isakov, E. (2007). Gait rehabilitation: a new biofeedback device for monitoring and enhancing weight-bearing over the affected lower limb. *Eura. Medicophys.* **43**, 21-26.

JudgeRoy, J. O., Davis, B., , III and Ounpuu, S. (1996). Step length reductions in advanced age: the role of ankle and hip kinetics. *J. Gerontol. A Biol. Sci. Med. Sci.* **51A**, M303-M312.

Kuo, A. D. and Donelan, J. M. (2009). Comment on "Contributions of the individual ankle plantar flexors to support, forward progression and swing initiation during walking" ((Neptune et al., 2001) and "Muscle mechanical work requirements during normal walking: the energetic cost of raising the body's center-of-mass is significant" (Neptune et al., 2004). *J. Biomech.* **42**, 1783-1785; author reply 1786-9.

Lelas, J. L., Merriman, G. J., Riley, P. O. and Kerrigan, D. C. (2003). Predicting peak kinematic and kinetic parameters from gait speed. *Gait Posture* **17**, 106-112.

Lewis, C. L. and Ferris, D. P. (2008). Walking with increased ankle pushoff decreases hip muscle moments. *J. Biomech*. **41**, 2082-2089.

McGibbon, C. A., Krebs, D. E. and Scarborough, D. M. (2003). Rehabilitation effects on compensatory gait mechanics in people with arthritis and strength impairment. *Arthritis. Rheum.* **49**, 248-254.

Meinders, M., Gitter, A. and Czerniecki, J. M. (1998). The role of ankle plantar flexor muscle work during walking. *Scand J. Rehabil. Med.* **30**, 39-46.

Mian, O. S., Thom, J. M., Ardigo, L. P., Narici, M. V. and Minetti, A. E. (2006). Metabolic cost, mechanical work, and efficiency during walking in young and older men. *Acta Physiol. (Oxf.)* **186**, 127-139.

Neptune, R. R., Kautz, S. A. and Zajac, F. E. (2001). Contributions of the individual ankle plantar flexors to support, forward progression and swing initiation during walking. *J. Biomech.* **34**, 1387-1398.

Neptune, R. R., Zajac, F. E. and Kautz, S. A. (2004). Muscle mechanical work requirements during normal walking: the energetic cost of raising the body's center-of-mass is significant. *J. Biomech.* **37**, 817-825.

Neptune, R. R., Clark, D. J. and Kautz, S. A. (2009a). Modular control of human walking: a simulation study. *J. Biomech.* **42**, 1282-1287.

Neptune, R. R., Zajac, F. E. and Kautz, S. A. (2009b). Author's Response to Comment on "Contributions of the individual ankle plantar flexors to support, forward progression and swing initiation during walking" (Neptune et al., 2001) and "Muscle mechanical work requirements during normal walking: the energetic cost of raising the body's center-of-mass is significant" (Neptune et al., 2004). *J. Biomech.* **42**, 1786-1789.

Ortega, J. D. and Farley, C. T. (2007). Individual limb work does not explain the greater metabolic cost of walking in elderly adults. *J. Appl. Physiol.* **102**, 2266-2273.

Piazza, S. J., Okita, N. and Cavanagh, P. R. (2001). Accuracy of the functional method of hip joint center location: effects of limited motion and varied implementation. *J Biomech*. **34**, 967-973.

Sawicki, G. S., Lewis, C. L. and Ferris, D. P. (2009). It pays to have a spring in your step. *Exerc. Sport Sci. Rev.* **37**, 130-138.

Selinger, J. C., O'Connor, S. M., Wong, J. D. and Donelan, J. M. (2015). Humans can continuously optimize energetic cost during walking. *Curr. Biol.* **25**, 2452-2456.

Silder, A., Heiderscheit, B. and Thelen, D. G. (2008). Active and passive contributions to joint kinetics during walking in older adults. *J. Biomech.* **41**, 1520-1527.

Toney, M. E. and Chang, Y.-H. (2016). The motor and the brake of the trailing leg in human walking: leg force control through ankle modulation and knee covariance. *Exp. Brain Res.* **234**, 3011-3023.

Wang, J., Hurt, C. P., Capo-Lugo, C. E. and Brown, D. A. (2015). Characteristics of horizontal force generation for individuals post-stroke walking against progressive resistive forces. *Clin. Biomech.* **30**, 40-45.

White, S. C. and Lifeso, R. M. (2005). Altering asymmetric limb loading after hip arthroplasty using real-time dynamic feedback when walking. *Arch. Phys. Med. Rehabil.* **86**, 1958-1963.

Winter, D. A., Patla, A. E., Frank, J. S. and Walt, S. E. (1990). Biomechanical walking pattern changes in the fit and healthy elderly. *Phys. Ther.* **70**, 340-347.

Zelik, K. E., Huang, T.-W. P., Adamczyk, P. G. and Kuo, A. D. (2014). The role of series ankle elasticity in bipedal walking. *J. Theor. Biol.* **346**, 75-85.