RESEARCH ARTICLE

Lower extremity joints and muscle groups in the human locomotor system alter mechanical functions to meet task demand

Daniel J. Kuhman[1],[*],[‡] and Christopher P. Hurt[1],[2],[*]

ABSTRACT

To facilitate movement through mechanically complex environments, terrestrial animals have evolved locomotor systems capable of flexibly altering internal mechanics to meet external demands. They do this by shifting imposed workloads between joints/muscle groups (central mechanical flexibility) and/or by altering the function of individual joints/ muscle groups (local mechanical flexibility). In human locomotion research, central mechanical flexibility is well established and regularly reported. Local mechanical flexibility at major lower extremity joints and muscle groups, however, has received relatively less attention. We used an emerging biomechanical analysis known as functional indexing to test the hypothesis that lower extremity joints and muscle groups within the human locomotor system alter their mechanical function to meet altered locomotor demands. Thirteen healthy adults walked across a range of speeds (0.8, 1.2, 1.6, 2.0 m s^{-1}) and slopes (0 deg, +5 deg, +10 deg) to determine whether hip, knee and ankle joints and their extensors and flexors altered their mechanical function in response to increased speed and slope. As walking speed increased, the knee and its extensors altered their function to behave more like mechanical springs while the ankle and its extensors altered their function to behave more like motors. As slope increased, all three joints and their extensors decreased spring- and damper-like behavior and increased motor-like behavior. Our results indicate that humans – similarly to many other terrestrial animals – utilize local mechanical flexibility to meet the demands of the locomotor task at hand.

KEY WORDS: Human, Locomotion, Biomechanics, Walking

INTRODUCTION

Locomotor capacity – the ability to effectively move through environments – is crucial for hunting, evading, foraging and migrating, all of which are important for animal survival. Terrestrial locomotor environments are mechanically complex. They commonly demand rapid changes in speed or direction of movement (i.e. acceleration, deceleration, maneuvering), negotiation of sloped surfaces, obstacle avoidance, adaptation to changing terrain or movement through constrained paths, all of which alter the mechanical demands on an animal's locomotor system (Franz et al., 2012; Gottschall and Kram, 2006; Qiao and Jindrich, 2016; Rosenblatt et al., 2015, 2014). To effectively negotiate these

complex environments, animals must have locomotor systems capable of flexibly altering internal mechanics to meet external demands. Previous studies of animal locomotion suggest that such mechanical flexibility presents itself both centrally and locally (Biewener and Gillis, 1999). Central mechanical flexibility represents the ability of an animal's nervous system to appropriately distribute the mechanical workload imposed by the environment between biological units [muscles, muscle–tendon units (MTUs) or muscle groups] within the locomotor apparatus. Local mechanical flexibility represents the capacity of each individual biological unit within the locomotor apparatus to alter its own mechanical function. The extent to which mechanical flexibility is utilized is likely an important metric of an animal's locomotor capacity and, as such, warrants scientific attention.

In their review of animal movement, Dickinson et al. (2000) described four basic mechanical functions that muscles in animal locomotor systems perform: strut, spring, motor and damper. Biological struts generate large forces while performing little mechanical work (e.g. isometric muscular contractions); springs store and return energy passively; motors perform positive work actively (e.g. concentric muscular contractions); dampers perform negative work actively (e.g. eccentric contractions) (Dickinson et al., 2000). These functions are thought to be governed primarily by muscle–tendon morphology. For example, MTUs comprising short, highly pinnate fibers interacting with long tendons (e.g. ankle extensors in many animals) are well suited for spring-like behavior, relying largely on elastic elements to store and return energy passively (Biewener, 2016; Roberts, 2002; Roberts and Azizi, 2011; Sawicki et al., 2009). MTUs comprising long muscle fibers interacting with short tendons (e.g. hip extensors in many animals) are better suited for motor- or damper-like behavior, performing positive or negative mechanical work actively via muscular contractions (Biewener, 1998; Biewener and Daley, 2007; Friederich and Brand, 1990; Sawicki et al., 2009). Many animals have MTUs of various morphologies and are capable of disproportionately distributing environmentally imposed workloads to the groups of MTUs best suited for performing the mechanical functions required by the locomotor task at hand (i.e. central mechanical flexibility) (Dickinson et al., 2000; Friederich and Brand, 1990). Additionally, some MTUs and muscle groups within animal locomotor systems have been shown to alter their mechanical functions to meet task demands (i.e. local mechanical flexibility) (Gabaldón et al., 2004; Roberts and Scales, 2004).

There is strong evidence that humans utilize central mechanical flexibility during locomotion. To walk uphill, humans disproportionately increase mechanical output from the hip extensors; to walk downhill, they disproportionately increase mechanical output from the knee extensors; running compared with walking at the same speed (2.0 m s^{-1}) involves a disproportionate increase in mechanical output from the ankle extensors (Alexander et al., 2017; Farris and Sawicki, 2012; Franz and Kram, 2014; Kuhman et al., 2018b; Lay et al.,

[1]Rehabilitation Science, University of Alabama at Birmingham, Birmingham, AL 35233, USA. [2]Department of Physical Therapy, University of Alabama at Birmingham, Birmingham AL 35233, USA.
*These authors contributed equally to this work

‡Author for correspondence (dkuhman@uab.edu)

D.J.K., 0000-0002-5495-7081

2006; Pickle et al., 2016; Sawicki et al., 2009). These findings indicate that humans regularly rely on central mechanical flexibility during locomotion. That is, they have the capacity to shift mechanical workloads between major muscle groups spanning lower extremity joints and regularly do so in response to altered locomotor demands.

There is also evidence that humans utilize local mechanical flexibility during locomotion. For example, shifts in kinetic profiles of individual joints have been observed during constant speed versus accelerated walking, uphill versus level walking and running, and walking versus running at the same speed, suggesting that joint function is partially dependent on task demand (Farris and Raiteri, 2017b; Farris and Sawicki, 2012; Franz and Kram, 2014; Qiao and Jindrich, 2016; Roberts and Belliveau, 2005; Schache et al., 2015). Additionally, ultrasound-based tracking of muscle dynamics suggests that local flexibility exists in individual muscles. For example, muscle fascicles within the triceps surae complex undergo greater shortening during fast versus slow walking, accelerated versus constant speed walking and running versus walking, suggesting increased motor-like function of these muscles during more mechanically demanding locomotor tasks (Farris and Raiteri, 2017a; Lai et al., 2015; Lichtwark et al., 2007). Although local mechanical flexibility can be inferred from previously reported joint kinetics and ultrasound-based muscle dynamics, quantifying and statistically testing the extent to which individuals utilize this flexibility is difficult without precise, quantitative measures of mechanical function.

Recently, a method that uses common biomechanical measures (joint moments and powers from inverse dynamics) was developed to quantify the extent to which a joint functions as a strut, spring, motor and damper – referred to as joint functional indices (Qiao and Jindrich, 2016). The few studies that have utilized this method confirmed that the human locomotor system – similarly to those in other animals – contains biological units that perform different mechanical functions. At the joint level, they found that the human hip acts primarily as a motor, the knee as a damper and the ankle as a spring during constant speed, level-ground walking (Farris and Raiteri, 2017b; Qiao and Jindrich, 2016). A more recent analysis quantified MTU-specific functional indices and found greater motor-like behavior of proximal versus distal MTUs (e.g. gluteus maximus versus gastrocnemii) (Lai et al., 2019). Although it was not the goal of these studies, they also presented evidence of local mechanical flexibility. Both Qiao and Jindrich (2016) and Farris and Raiteri (2017b) found that the human ankle functioned primarily as a spring during constant speed walking but as a motor during accelerated walking. These observations provide evidence that local mechanical flexibility exists within the human locomotor system; however, it was only observed at a single joint – likely due to the relatively unchallenging task of accelerated walking. Challenging the human locomotor system to a greater extent will better test whether local mechanical flexibility is utilized by other major lower extremity joints and whether the functional indexing method captures this flexibility. Additionally, it is important to extend the functional indexing analysis from joints to individual muscle groups, which could provide insight into how various muscle groups function during locomotion and which muscle group drives any observed changes at the whole joint level.

To test whether local mechanical flexibility exists within the human locomotor system, we quantified joint and muscle group mechanical functions during tasks that should have altered functions in specific ways. Uphill walking requires that net positive work be done to lift the center of mass with each step (Alexander et al., 2017; Franz et al., 2012). Accordingly, uphill walking is achieved with

increased positive and decreased negative work from the three major lower extremity joints and is therefore likely associated with increased motor-like and decreased damper-like and/or spring-like function from these joints (Alexander et al., 2017). Faster walking speeds, so long as they are kept constant, are accomplished by concomitant increases in total positive and negative work, making it less clear whether changing speed will also alter mechanical functions. However, previously published joint power profiles and work loops (joint moment versus angular displacement) suggest that some lower extremity joints – especially the ankle – may alter their functions in response to altered walking speeds (Farris and Sawicki, 2012; Hansen et al., 2004; Jin and Hahn, 2018; Schache et al., 2015). Quantifying strut, spring, motor and damper behavior of the major lower extremity joints and muscle groups across a wider range of locomotor tasks will more thoroughly test the extent to which humans utilize local mechanical flexibility. The purpose of this study was to determine whether the mechanical functions of major lower extremity joints and muscle groups within the human locomotor system change when walking speed and slope are altered. We hypothesized that, as walking speed increased, the ankle and its extensors would exhibit decreased spring- and increased motor-like function. It was unclear, however, whether knee or hip functions would change across level-ground walking speeds. We also hypothesized that all three joints and their muscle groups – especially the extensors – would exhibit decreased spring- and damper-like functions and increased motor-like function during uphill compared with level ground walking.

MATERIALS AND METHODS
Human participants
Thirteen healthy, young adults (8 female; mean±s.d.: age=25.2±2.1 years, mass=73.0±12.4 kg, height=1.7±0.1 m) participated in this study. To ensure that our sample represented a healthy, non-impaired population, we pre-set the following exclusion criteria: lower extremity injury in the 6 months prior to participation, history of lower extremity joint surgery, any cardiovascular, pulmonary, neuromuscular or orthopedic disorder that could impair walking. This study was approved by the University of Alabama at Birmingham Institutional Review Board and all participants provided written informed consent prior to performing any aspect of the protocol.

Experimental setup and equipment
Kinematic and ground reaction force (GRF) data were collected simultaneously using 8 infrared cameras (Vicon Motion Systems, Denver, CO, USA; 100 Hz) and a dual-belt force-instrumented treadmill (Motek Link, Amsterdam, Netherlands; 1000 Hz), respectively. Vicon Nexus software, Visual 3D (C-Motion Inc., Rockville, MD, USA) and laboratory software written in MATLAB (MathWorks Inc., Natick, MA, USA) were used to collect, process and analyze biomechanical data.

Experimental protocol
Participants performed treadmill walking trials at 0.8 m s^{-1}, 1.2 m s^{-1}, 1.6 m s^{-1} and 2.0 m s^{-1} with the treadmill at 0 deg and at 1.2 m s^{-1} with the treadmill at 0 deg, +5 deg and +10 deg (+ denotes inclination). In each condition, participants walked ~60 s and data were collected for the last 20 s. Brief periods of rest were given between trials. For trials performed at 2.0 m s^{-1}, participants were instructed specifically to maintain a walking gait, as this speed is commonly reported as the point at which individuals transition to a run (Beuter and Lalonde, 1988; Diedrich and Warren, 1995; Hreljac, 1993) – this was enforced visually during data acquisition

and confirmed post-processing by identifying periods of double support in all steps included in our analysis.

Passive reflective markers were used to define and track movement of the upper arms, forearms, trunk, pelvis, thighs, shanks and feet. Upper arms were defined and tracked by the acromion process, the lateral epicondyle of the humerus and a single marker placed on the biceps muscle. Forearms were defined and tracked by the lateral epicondyle of the humerus, the styloid process of the radius and a single marker placed mid-forearm. The trunk was defined and tracked by left/right acromion processes and left/right posterior superior iliac spines, the manubrium and the 7th cervical vertebra. The pelvis was defined and tracked by markers placed on the left/right anterior and posterior superior iliac spines. Thigh segments were defined by left/right greater trochanters and the medial/lateral femoral epicondyles and tracked using the greater trochanter, lateral femoral epicondyle and a marker placed on the anterior aspect of the thigh. Shank segments were defined by medial/lateral femoral epicondyles and medial/lateral malleoli and tracked using lateral femoral epicondyle, lateral malleolus and a marker placed on the anterior aspect of the shank. Feet segments were defined by medial/lateral malleoli and first/fifth metatarsophalangeal (MP) joints and tracked using markers on the first/fifth MP joints and a single marker placed on the heel.

Data analysis
Kinematic and GRF data were filtered using low-pass Butterworth filters with cutoff frequencies of 6 and 12 Hz, respectively, to remove signal noise (Antonsson and Mann, 1985; Kram et al., 1998; Winter et al., 1974). Joint angles, moments and powers were estimated using Visual 3D. We calculated strut, spring, motor and damper indices at the hip, knee and ankle during the support phase to characterize mechanical function during walking. We used analyses similar to those described by Qiao and Jindrich (2016) and Farris and Raiteri (2017b; however, our analyses were distinct in that we calculated functional indices not only for each joint as a whole, but also separately for the extensors and flexors at the hip and knee and for the extensors (i.e. plantarflexors) at the ankle. Functional indices for the ankle flexors (i.e. dorsiflexors) were not calculated, as this muscle group is active for only a small amount of the support phase. These analyses quantify, by percentage, the extent to which each joint and muscle group functions as a strut, spring, motor and damper. The equations are performed such that the sum of percentages of each function equals 100% at each joint and muscle group. Essentially, these analyses are used to functionally characterize the mechanical work performed by joints and muscle groups during locomotion. For total joint calculations, these indices were computed for the entire support phase. For joint extensor (flexor) calculations, the indices were computed for phases of support where net extensor (flexor) moments were present. Joint extensor and flexor onset and offset times were determined using zero crossings on each joint's support phase moment curve (see example in Fig. 1). These zero crossings were identified automatically using a custom-built MATLAB function and confirmed visually during data analysis. At all joints, positive moments indicated net internal extensor action and negative moments indicated net internal flexor action. Thus, periods of support with positive moments were used to calculate functional indices for joint extensors and periods of support with negative moments were used to calculate functional indices for joint flexors. This method allows for joint and muscle group functional indices to be calculated on each step. It is important to note that these indices were calculated using net joint moments estimated from inverse
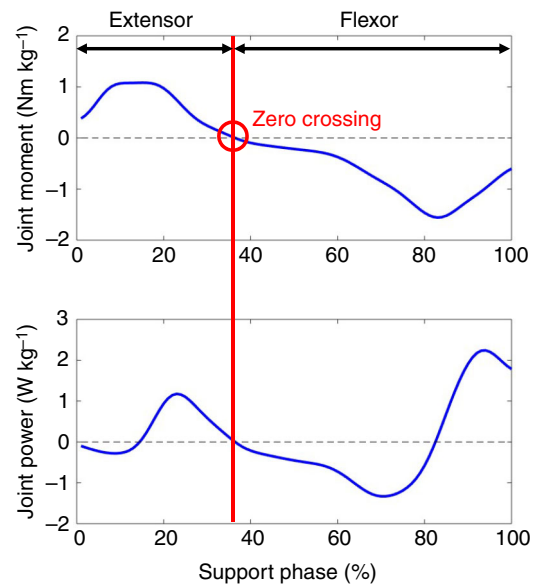

Fig. 1. The use of zero crossings on a joint moment curve to identify periods of extensor and flexor action. The data represent hip joint moment (top) and power (bottom); however, functional indices were computed independently at each joint. Functional indices can be calculated for the entire joint using moment and power data across the entire support phase: for extensors, using moment and power data from the periods of support where the net moment is positive, and for the flexors, using moment and power data from periods of support where the net moment is negative. This method allows functional indices for entire joints and extensor and flexor groups to be calculated on a per-step basis.

dynamics analyses, which can be influenced by forces not associated with the anatomical groups alluded to using the terms 'extensor' and 'flexor' (e.g. agonist/antagonist co-contraction, biarticular muscles, connective tissue, gravitational moments) (Zajac, 1993). Thus, 'muscle groups' refer to functional rather than anatomical groups of muscles. Functional indexing analyses were performed using custom software written in MATLAB.

Strut index
The strut index was calculated as the ratio of joint-level mechanical work over moment impulse during periods of interest (Eqns 1, 2, 3). The strut index will be high when large moments occur concurrently with little mechanical work.

$$I_{\text{strut,joint}} = \max\left(1 - \frac{(t_{\text{TO}} - t_{\text{HS}}) \int_{\text{TO}}^{\text{HS}} |P_{\text{joint}}| dt}{\int_{\text{TO}}^{\text{HS}} |\mathbf{M}_{\text{joint}}| dt}, 0\right) \times 100\%, \quad (1)$$

$$I_{\text{strut,ext}} = \max\left(1 - \frac{(t_{\text{ext off}} - t_{\text{ext on}}) \int_{\text{ext off}}^{\text{ext on}} |P_{\text{joint}}| dt}{\int_{\text{ext off}}^{\text{ext on}} |\mathbf{M}_{\text{joint}}| dt}, 0\right) \times 100\%, \quad (2)$$

$$I_{\text{strut,flx}} = \max\left(1 - \frac{(t_{\text{flx off}} - t_{\text{flx on}}) \int_{\text{flx off}}^{\text{flx on}} |P_{\text{joint}}| dt}{\int_{\text{flx off}}^{\text{flx on}} |\mathbf{M}_{\text{joint}}| dt}, 0\right) \times 100\%, \quad (3)$$

where $I_{\text{strut,joint}}$ is the strut index for the entire joint; $I_{\text{strut,ext}}$ and $I_{\text{strut,flx}}$ are strut indices for the extensors and flexors, respectively; t_{TO} is time of toe-off and t_{HS} is time of heel strike; $t_{\text{ext on}}$ and $t_{\text{ext off}}$ are time of joint extensor moment onset and offset, respectively; $t_{\text{flx on}}$ and $t_{\text{flx off}}$ are time of joint flexor moment onset and offset, respectively; P_{joint} is joint power; $\mathbf{M}_{\text{joint}}$ is joint moment.

Spring index

The spring index represents potential storage and return of energy at a joint or muscle group (Eqns 4, 5, 6). Spring-like behavior is defined as any period of negative work ('potential storage' work; $W^-_{\text{pot. storage}}$) followed immediately by positive work ('potential return' work; $W^+_{\text{pot. return}}$). Potential storage and potential return work are referred to as 'compression' and 'thrust' work, respectively, by Qiao and Jindrich (2016) and Farris and Raiteri (2017b). We use altered terminology because, in general, biological tissues have the potential to store energy when lengthened (rather than compressed) and return energy during subsequent shortening (rather than thrusting). We included the term 'potential' (abbreviated 'pot.') because these equations assume that all negative work can be stored and subsequently returned as positive work when in reality, some negative work will not be restored, even in highly efficient tissues (Zelik and Franz, 2017). Note that, although we use altered terminology, the equations themselves are not different from those used by Qiao and Jindrich (2016) and Farris and Raiteri (2017b). When multiple instances of such behavior occurred at a joint or within a muscle group, $W^-_{\text{pot. storage}}$ was calculated as the sum of work from all periods of potential storage and $W^+_{\text{pot. return}}$ was calculated as work from all periods of potential return.

$$I_{\text{spring, joint}} = \frac{2 \cdot \min(|W^-_{\text{pot. storage,joint}}|, |W^+_{\text{pot. return,joint}}|)}{|W^-_{\text{joint}}| + |W^+_{\text{joint}}|} \times (100\% - I_{\text{strut,joint}}), \tag{4}$$

$$I_{\text{spring, ext}} = \frac{2 \cdot \min(|W^-_{\text{pot. storage,ext}}|, |W^+_{\text{pot. return,ext}}|)}{|W^-_{\text{ext}}| + |W^+_{\text{ext}}|} \times (100\% - I_{\text{strut,ext}}), \tag{5}$$

$$I_{\text{spring, flx}} = \frac{2 \cdot \min(|W^-_{\text{pot. storage,flx}}|, |W^+_{\text{pot. return,flx}}|)}{|W^-_{\text{flx}}| + |W^+_{\text{flx}}|} \times (100\% - I_{\text{strut,flx}}), \tag{6}$$

where W^- represents the negative work performed during the period of interest and W^+ represents the positive work performed. In all instances, mechanical work was calculated as the integral of joint power over specific periods of interest (e.g. period of potential storage, period of potential return, etc.).

Motor index

The motor index represents positive work that is not potentially performed via spring-like behavior (Eqns 7, 8, 9). The motor index will be high when large amounts of positive work are not preceded by large amounts of negative work.

$$I_{\text{motor,joint}} = \frac{|W^+_{\text{joint}}| - \min(|W^-_{\text{pot. storage,joint}}|, |W^+_{\text{pot. return,joint}}|)}{|W^-_{\text{joint}}| + |W^+_{\text{joint}}|} \times (100\% - I_{\text{strut,joint}}). \tag{7}$$

$$I_{\text{motor,ext}} = \frac{|W^+_{\text{ext}}| - \min(|W^-_{\text{pot. storage,ext}}|, |W^+_{\text{pot. return,ext}}|)}{|W^-_{\text{ext}}| + |W^+_{\text{ext}}|} \times (100\% - I_{\text{strut,ext}}). \tag{8}$$

$$I_{\text{motor,flx}} = \frac{|W^+_{\text{flx}}| - \min(|W^-_{\text{pot. storage,flx}}|, |W^+_{\text{pot. return,flx}}|)}{|W^-_{\text{flx}}| + |W^+_{\text{flx}}|} \times (100\% - I_{\text{strut,flx}}). \tag{9}$$

Damper index

The damper index represents negative work that is not potentially stored for spring-like behavior (Eqns 10, 11, 12). The damper index will be high when large amounts of negative work are not immediately followed by large amounts of positive work.

$$I_{\text{damper,joint}} = \frac{|W^-_{\text{joint}}| - \min(|W^-_{\text{pot. storage,joint}}|, |W^+_{\text{pot. return,joint}}|)}{|W^-_{\text{joint}}| + |W^+_{\text{joint}}|} \times (100\% - I_{\text{strut,joint}}). \tag{10}$$

$$I_{\text{damper,ext}} = \frac{|W^-_{\text{ext}}| - \min(|W^-_{\text{pot. storage, ext}}|, |W^+_{\text{pot. return,ext}}|)}{|W^-_{\text{ext}}| + |W^+_{\text{ext}}|} \times (100\% - I_{\text{strut,ext}}). \tag{11}$$

$$I_{\text{damper,flx}} = \frac{|W^-_{\text{flx}}| - \min(|W^-_{\text{pot. storage,flx}}|, |W^+_{\text{pot. return,flx}}|)}{|W^-_{\text{flx}}| + |W^+_{\text{flx}}|} \times (100\% - I_{\text{strut,flx}}). \tag{12}$$

All variables were calculated for 10 steps on both left and right legs for each condition in each participant. For some participants in some conditions 10 steps per leg could not be analyzed due to consistently inappropriate foot placement on the treadmill (e.g. the left foot contacted the right treadmill belt). In such cases, as many steps as possible were analyzed. We refrained from providing corrective feedback in these cases to ensure that participants did not purposefully change their gait to maintain appropriate foot placement. For each participant, data were averaged across both legs in each condition. Data were then averaged across all participants in each condition for statistical analyses.

Statistical analysis

To address our hypotheses, we performed a series of two-way repeated measures analyses of variance (ANOVAs). To test whether mechanical function at each joint and muscle group changed with walking speed, we performed a two-way ANOVA with two within subject factors: functional index (strut, spring, motor, damper) and speed (0.8 m s^{-1}, 1.2 m s^{-1}, 1.6 m s^{-1}, 2.0 m s^{-1}). To test whether mechanical function at each joint and muscle group changed with slope, we performed a two-way ANOVA with two within-subject factors: functional index (strut, spring, motor, damper) and slope (0 deg, +5 deg, +10 deg). Significant interactions in these analyses indicate that functional indices are altered at different rates across speeds and slopes (respectively), suggesting altered mechanical function in response to altered task demand. The significance threshold for all tests were set at $\alpha = 0.05$. Statistical analyses were conducted using SPSS v. 25 (IBM, Armonk, NY, USA).

RESULTS

Changes in mechanical function at faster walking speeds

Although non-primary mechanical functions (i.e. functions with <15%) were altered with speed, primary functions of the hip, and its extensors and flexors, remained similar across all speeds tested (Fig. 2A and Fig. 3A,B). For the hip as a whole, we observed a significant interaction of index and speed ($P<0.001$), however this interaction appeared to be driven by alterations in non-primary functions while the primary function – spring – remained the same across all speeds (~50% at 0.8 m s^{-1} to ~51% at 2.0 m s^{-1}). For the hip extensors, we observed a significant interaction ($P<0.001$) that appeared to be driven by non-primary functions while the primary
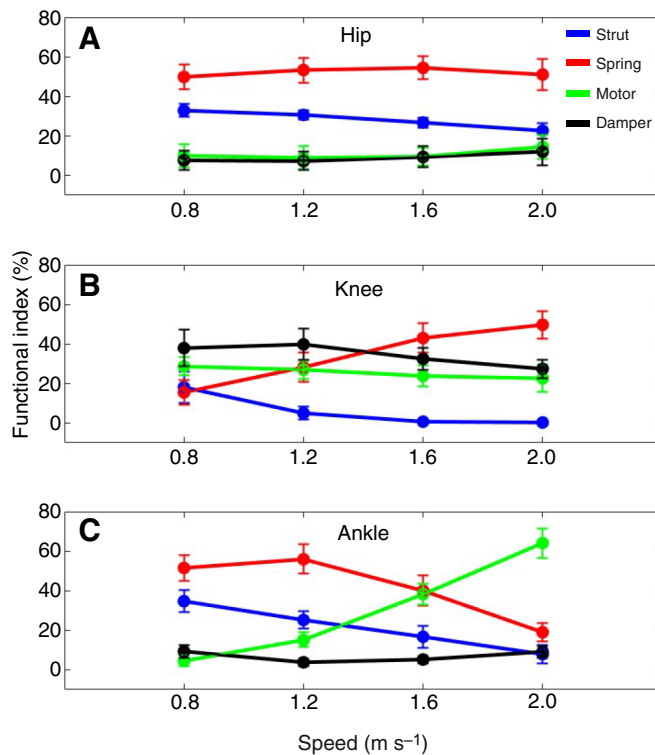
Fig. 2. Whole joint functional indices at the hip, knee and ankle across all level-ground walking speeds. Group (n=13) means±95% confidence intervals (CIs) for hip (A), knee (B) and ankle (C). In all graphs, non-overlapping 95% CIs indicate significant differences between the means (P<0.05). The hip functions primarily as a spring across all speeds. At the knee, as speed increased, spring-like function increases and damper-like function decreases. At the ankle, as speed increases, motor-like function increases and spring-like function decreases.

function – strut – remained high and relatively stable across all speeds (~86% at 0.8 m s^{-1} to ~76% at 2.0 m s^{-1}). For the hip flexors, we observed a significant interaction (P<0.01) that appeared to be driven by non-primary functions while the primary functions – strut and spring – remained relatively constant across all speeds (strut: ~49% at 0.8 m s^{-1} to ~47% at 2.0 m s^{-1}; spring: ~41% at 0.8 m s^{-1} to ~38% at 2.0 m s^{-1}).

The knee joint as a whole, and its extensors, decreased damper-like behavior and increased spring-like behavior as walking speed increased (Fig. 2B and Fig. 3C) while the knee flexors functioned primarily as struts across all speeds (Fig. 3D). For the knee as a whole, we observed a significant interaction of index and speed (P<0.001) that appeared to be driven by decreased damper, motor and strut indices and an increased spring index (~15% at 0.8 m s^{-1} to ~50% at 2.0 m s^{-1}). For the knee extensors, we observed a significant interaction (P<0.001) that appeared to be driven by a decreased damper index (~54% at 0.8 m s^{-1} to ~29% at 2.0 m s^{-1}) and an increased spring index (~5% at 0.8 m s^{-1} to ~31% at 2.0 m s^{-1}). For the knee flexors, we observed a significant interaction (P<0.001) that appeared to be driven by non-primary functions while strut-like behavior remained their primary function across all speeds.

The ankle joint as a whole, and its extensors, functioned less as springs and struts and more as motors as speed increased (Fig. 2C and Fig. 3E). For the ankle as a whole, we observed a significant interaction of index and speed (P<0.001) that appeared to be driven by decreased spring (~51% at 0.8 m s^{-1} to ~19% at 2.0 m s^{-1}) and

strut (~35% at 0.8 m s^{-1} to 8% at 2.0 m s^{-1}) indices and an increased motor index (~5% at 0.8 m s^{-1} to ~64% at 2.0 m s^{-1}). For the ankle extensors, we observed a significant interaction (P<0.001) that appeared to be driven by decreased spring (~43% at 0.8 m s^{-1} to ~16% at 2.0 m s^{-1}) and strut (~47% at 0.8 m s^{-1} to 26% at 2.0 m s^{-1}) indices and an increased motor index (~4% at 0.8 m s^{-1} to ~56% at 2.0 m s^{-1}).

Changes in mechanical function during uphill walking

The hip joint as whole, and its extensors, adopted more motor-like behavior as slope increased (Fig. 4A and Fig. 5A) while the flexors exhibited consistently high strut-like behavior across all slopes (Fig. 5B). For the hip as a whole, we observed a significant interaction of index and slope (P<0.001), with decreased spring (~53% at 0 deg to ~34% at +10 deg) and increased motor (~9% at 0 deg to ~63% at +10 deg) behavior as slope increased. For the hip extensors, we observed a significant interaction (P<0.001), with decreased strut (~85% at 0 deg to ~31% at +10 deg) and increased motor (~13% at 0 deg to ~69% at +10 deg) behavior as slope increased. For the hip flexors, we observed a significant interaction (P<0.001), which appeared to be associated with changes in non-primary functions (motor and damper) but also with increased strut (~47% at 0 deg to 57% at +10 deg) and decreased spring (42% at 0 deg to 34% at +10 deg) behavior with increasing slope.

The knee joint as a whole, and its extensors, decreased damper- and increased strut- and motor-like function as slope increased (Fig. 4B and Fig. 5C) while the knee flexors functioned primarily as struts across all slopes (Fig. 5D). For the knee joint as a whole, we observed a significant interaction of index and slope (P<0.001), with decreased damper (~40% at 0 deg to ~8% at +10 deg) and increased spring (~28% at 0 deg to ~41% at +10 deg) and motor (~27% at 0 deg to ~47% at +10 deg) indices as slope increased. For the knee extensors, we observed a significant interaction (P<0.001), with spring (~13% at 0 deg to 3% at +10 deg) and especially damper (~52% at 0 deg to ~8% at +10 deg) indices decreasing and strut (~32% at 0 deg to ~43% at +10 deg) and especially motor (~4% at 0 deg to ~46% at +10 deg) indices increasing as slope increased. For the knee flexors, we observed a significant interaction (P<0.001) that appeared to be driven by non-primary functions while strut-like behavior remained their primary function across all slopes.

The ankle joint as a whole, and its extensors, decreased spring- and strut-like behaviors and increased motor-like behavior as slope increased (Fig. 4C and Fig. 5E). For the ankle joint as a whole, we observed a significant interaction of index and slope (P<0.001), with decreased spring (~56% at 0 deg to ~11% at +10 deg) and strut (~25% at 0 deg to ~17% at +10 deg) indices and an increased motor (~15% at 0 deg to ~70% at +10 deg) index as slope increased. For the ankle extensors, we observed a significant interaction (P<0.001), with decreased spring (~46% at 0 deg to ~10% at +10 deg) and strut (~40% at 0 deg to ~28% at +10 deg) indices and an increased motor index (~12% at 0 deg to ~61% at +10 deg) as slope increased.

DISCUSSION

The purpose of this study was to determine whether mechanical functions of major lower extremity joints and muscle groups within the human locomotor system changed when walking speed and slope were altered. More broadly, we were interested in determining the extent to which humans utilized local mechanical flexibility during locomotion. Our results fully supported our hypothesis that faster walking speeds would result in decreased spring- and
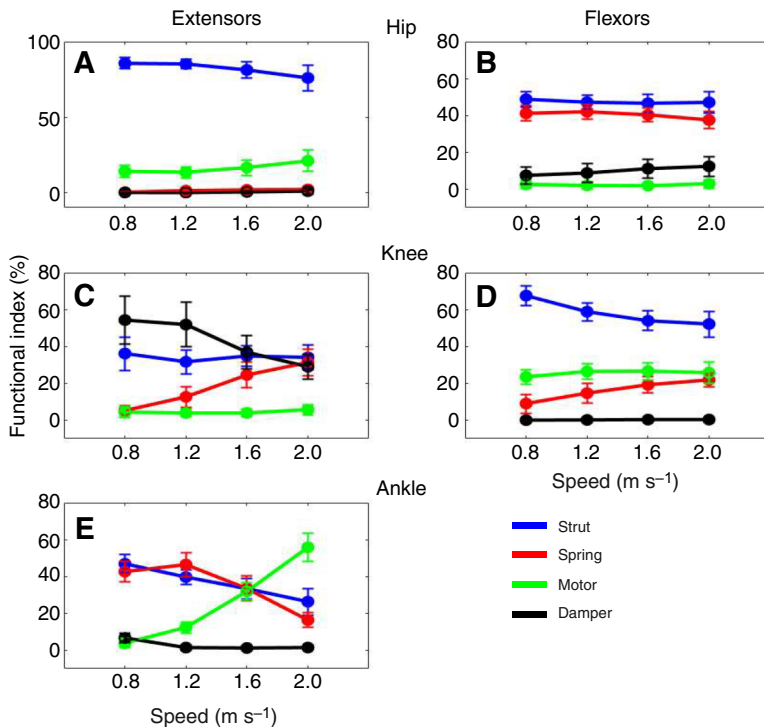
Fig. 3. Extensor and flexor muscle group functional indices at the hip, knee and ankle across all level-ground walking speeds. Group (*n*=13) means±95% confidence intervals (CIs) for hip (A,B), knee (C,D) and ankle (E). Functional indices for the ankle flexors (i.e. dorsiflexors) were not computed, as this muscle group is active for only a short period of the support phase immediately after heel strike. In all graphs, non-overlapping 95% CIs indicate significant differences between the means (*P*<0.05). At the hip, the extensors function primarily as a strut and the flexors function as both a strut and a spring across all speeds. The knee extensors alter their function as walking speed increased while the knee flexors function primarily as a strut across all speeds. At the slower two speeds, the knee extensors function as a damper and strut. As speed increases, the knee extensors increase spring-like function and decrease damper-like function. The ankle extensors function primarily as a spring and a strut at the slower two speeds and increase motor-like behavior as speed increases.

increased motor-like function of the ankle and its extensors. In addition to the across-speed changes at the ankle, we observed decreased damper-like and increased spring-like function of knee

Fig. 4. Whole joint functional indices at the hip, knee and ankle across all slopes. Group (*n*=13) means±95% confidence intervals (CIs) for hip (A,B), knee (C,D) and ankle (E). Participants walked at 1.2 m s⁻¹ on each slope. In all graphs, non-overlapping 95% CIs indicate significant differences between the means (*P*<0.05). As uphill slope gets steeper, the hip functions less as a spring and more as a motor, the knee functions less as a damper and more as a spring and motor, and the ankle functions less as a spring and more as a motor.

and its extensors as walking speed increased. No across-speed functional changes were observed at the hip. We also hypothesized that all three joints and their muscle groups – especially the extensors – would exhibit decreased spring- and/or damper-like function and increased motor-like function during uphill walking. Our results fully supported this hypothesis, as all three joints and their extensors behaved more like motors during uphill walking. Combined, our results provide stronger evidence that, similarly to other terrestrial animals, local mechanical flexibility is utilized within the human locomotor system. We are the first to use the functional indexing method to statistically test whether mechanical functions of joints and muscle groups change in response to altered task demand. The approach used here is non-invasive and relatively easy to implement, making it a promising paradigm for future studies of animal locomotion.
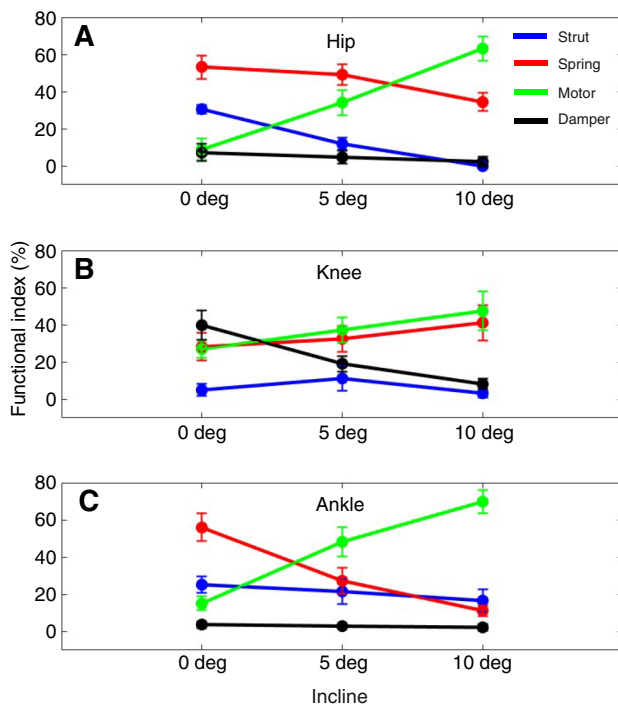
Functional changes at faster walking speeds

Of the three major lower extremity joints included here, the hip was the only one to maintain a single function across all speeds. The hip as a whole functioned primarily as a spring across all speeds, which is somewhat surprising given the morphology of the major muscles spanning this joint and the view that a proximal-to-distal gradient of function exists within many animal locomotor systems (Biewener, 1998; Lai et al., 2019). According to these views, it would seem more likely that the hip would exhibit high motor- and/or damper-like behavior, as the extensors and flexors of this proximal joint are primarily composed of long muscle fibers interacting with short tendons (Biewener, 2016; Biewener and Daley, 2007; Dutto et al., 2006; Friederich and Brand, 1990; Sawicki et al., 2009). However, the hip flexors perform a large amount of negative work in mid-support proceeded immediately by positive work in late support (Fig. 6). In the functional indexing equations, this joint power profile resulted in high spring-like behavior from the hip flexors, which apparently drives the function of the joint as a whole. Although contrary to traditional views, we are not the first to report that muscles at the hip can act as mechanical springs during walking
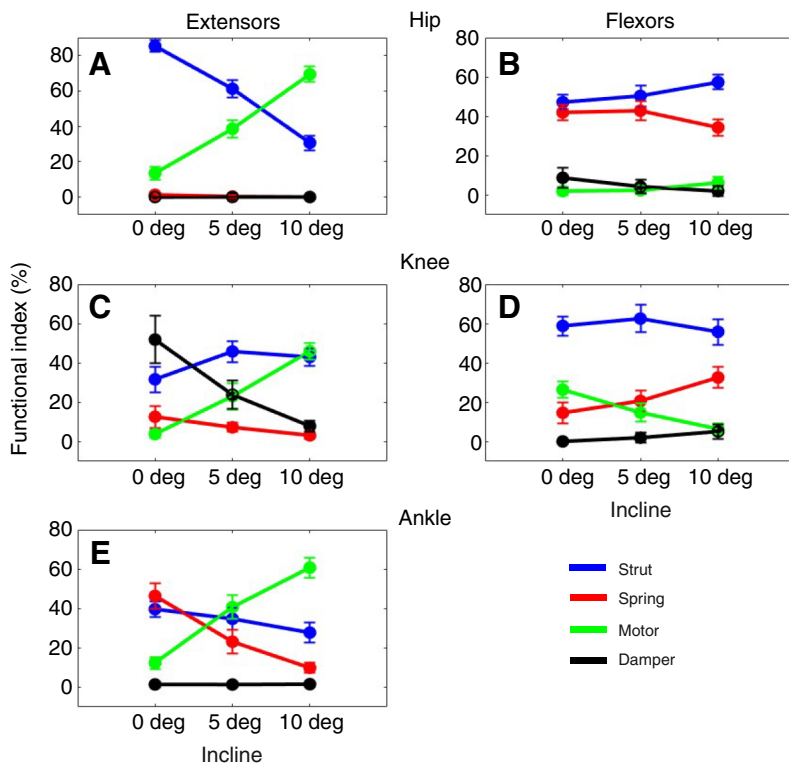
Fig. 5. Extensor and flexor muscle group functional indices at the hip, knee and ankle across all slopes. Group (n=13) means±95% confidence intervals (CIs) for hip (A,B), knee (C,D) and ankle (E). Participants walked at 1.2 m s^{-1} on each slope. Functional indices for the ankle flexors (i.e. dorsiflexors) were not computed, as this muscle group is active for only a short period of the support phase immediately after heel strike. In all graphs, non-overlapping 95% CIs indicate significant differences between the means (P<0.05). The hip extensors function less as a strut and more as a motor as uphill slope gets steeper. The hip flexors function as both a strut and a spring at 0 deg and +5 deg but more clearly as a strut at +10 deg. The knee extensors function less as a damper and more as a strut and motor (with no clear difference between the two at +10 deg) as uphill slope gets steeper. The knee flexors function as a strut across all slopes. The ankle extensors function less as a spring and strut and more as a motor as uphill slope gets steeper.

(Hines et al., 2018; Lai et al., 2019; Silder et al., 2008; Simonsen et al., 2012; Whittington et al., 2008). For example, Whittington et al. (2008) reported that ~58% of the positive work performed by the hip flexors in late support was the result of passive energy storage and return. Elastic elements other than tendon (e.g.

sarcolemma, perimysium and structural proteins such as titan) may allow a muscle or muscle group to behave as a spring, even if it does not have the muscle–tendon morphology traditionally considered optimal for spring-like behavior (Blackburn et al., 2004; Gajdosik, 2001; Schleip et al., 2006). Given that muscles
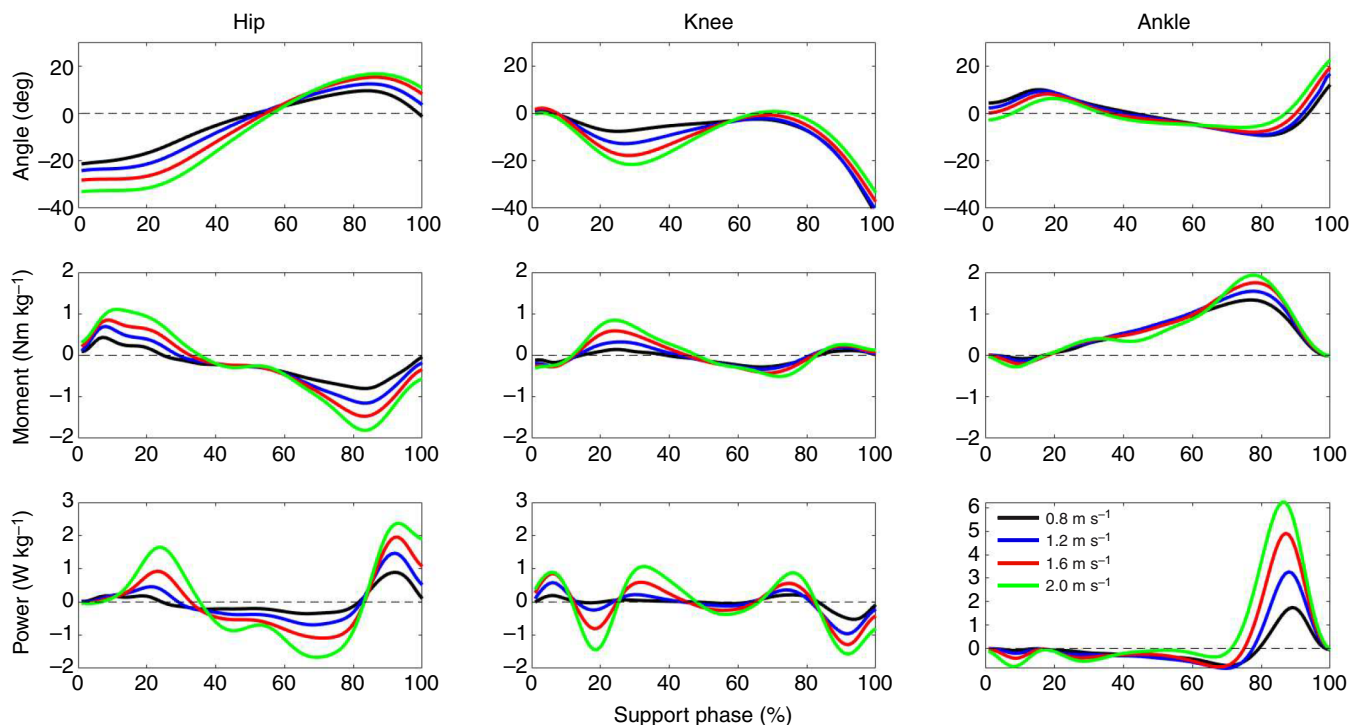

Fig. 6. Ensemble curves for hip, knee and ankle joint angles, moments and powers across all level-ground walking speeds. Group (n=13) data represent the support phase only and moments and powers were normalized to body mass. 0.8 m s^{-1} (black lines), 1.2 m s^{-1} (blue lines), 1.6 m s^{-1} (red lines) and 2.0 m s^{-1} (green lines).

spanning the hip contribute a large amount of the mechanical work performed during the support phase of walking (∼25–30% of the total positive and total negative work), it would not be entirely surprising if these muscles evolved to perform this work passively rather than actively as an energy conservation mechanism (Alexander et al., 2017; Farris and Sawicki, 2012). Alternatively, this finding may highlight a weakness in the functional indexing method – namely, that the spring index calculation assumes 100% of negative work followed immediately by positive work can be conserved passively, which is unrealistic in even highly efficient biological tissues (e.g. Achilles tendon) (Zelik and Franz, 2017). Although the hip flexors perform a large amount of negative work immediately proceeded by positive work, it is possible that some or even most of this work is performed actively rather than passively (i.e. they act as dampers and then motors rather than as a spring). Indeed, intramuscular electromyography analysis suggests that the hip flexor muscles are active during the mid and late support phases (Andersson et al., 1997). Future efforts toward making the functional indexing method more biologically realistic are warranted. The analysis could be improved by adding an 'efficiency' term to the spring index equation that regulates how much mechanical work could realistically be conserved passively. To quantify these efficiency terms while maintaining the non-invasive nature of the analysis, investigators may draw inspiration from the passive moment methods used by Whittington et al. (2008) to determine the extent to which passive elements at each joint contribute to kinetics measured during walking.

Across-speed results at the knee and ankle support the notion that local mechanical flexibility is utilized within the human locomotor system when altering level-ground walking speed. At the knee, we observed decreased damper- and motor-like behavior, and increased spring-like behavior as speed increased. This joint-level change appeared to be driven primarily by decreased damper- and increased spring-like behavior from the knee extensors; however, the flexors also exhibited slightly increased spring-like behavior at faster speeds (from ∼9% at 0.8 m s^{-1} to ∼22% at 2.0 m s^{-1}). Similarly to the muscles spanning the hip, it was surprising to find large amounts of spring-like behavior at the knee because, based on the traditional morphology-function relationship, it seems more likely that this joint and its major muscle groups should exhibit high motor- and/or damper-like behavior. Although this was the case while individuals walked at 0.8 m s^{-1} and 1.2 m s^{-1}, large amounts of spring-like behavior emerged at faster speeds, especially from the knee extensors. Recently, the functional indexing methods used here were combined with computational simulations of human walking to derive muscle- and MTU-specific mechanical functions and found that the biarticular rectus femoris acts more like a damper while the uniarticular vastus lateralis acts more like a spring (Lai et al., 2019). In line with this, evidence recently emerged highlighting the importance of series elastic elements – and thus, the spring-like capacity – of the vastus lateralis during human locomotion (Bohm et al., 2018). Those authors were surprised to find that muscle fibers in the vastus lateralis acted near isometrically while walking at 1.5 m s^{-1}, suggesting that much of the mechanical work at the joint was being performed via spring-like behavior. In the current study, it is possible that speeds beyond 1.2 m s^{-1} elicited disproportionately larger contributions from the uniarticular compared with biarticular knee extensor muscles, resulting in higher spring-like behavior from the muscle group as a whole. Our knee joint results might also be explained by the same methodological limitations discussed above (related to the high spring-like behavior observed from the hip flexors).

In support of our first hypothesis, we observed a switch from primarily spring- to motor-like behavior from the ankle joint and its extensors as walking speed increased. These findings are consistent with previous observations of increased positive and decreased or unchanged negative work at the human ankle with faster walking speeds (Ebrahimi et al., 2017; Jin and Hahn, 2018; Schache et al., 2015). We also observed increased positive (from 0.17±0.02 J kg^{-1} at 0.8 m s^{-1} to 0.51±0.10 J kg^{-1} at 2.0 m s^{-1}) and decreased negative (from −0.20±0.04 J kg^{-1} at 0.8 m s^{-1} to −0.13± 0.04 J kg^{-1} at 2.0 m s^{-1}) work at faster speeds. These results are also similar to previously published ankle joint work loops (moments versus angular positions), which suggest increased motor-like behavior at faster speeds (Hansen et al., 2004; Jin and Hahn, 2018). They are also consistent with previous biomechanical analyses of other terrestrial animals. In wild turkeys (*Meleagris gallopavo*), the ankle joint performs disproportionately more positive than negative work at increasingly higher rates of level-ground acceleration, suggesting increased motor-like and decreased spring-like behavior at the joint (Roberts and Scales, 2004). Muscle-specific work in wild turkeys adds further support to this idea: the lateral gastrocnemius – which is morphologically best suited to act as a mechanical spring – acts increasingly as a motor at faster level-ground running speeds (Gabaldón et al., 2004). Interestingly, speed-induced local mechanical flexibility at distal joints has not been shown in all terrestrial animals. For example, trotting speed appears to have little effect on the spring-like power profiles of distal joints in horse (*Equus caballus*) limbs (Dutto et al., 2006). Similarly, net work at the ankle joint of the goat hindlimb (which exhibits spring-like power profiles during both trotting and galloping) does not change with speed during level-ground locomotion (Arnold et al., 2013). Further research is warranted to determine the underlying reasons for these across-species differences in utilization of local mechanical flexibility and the potential implications of this utilization on locomotor capacity. We hope that the functional indexing method used here will facilitate such research.

Our across-speed observations at the ankle have potential implications for other commonly explored biomechanical phenomena. For example, the fastest speed tested here (2.0 m s^{-1}) is commonly considered the point at which individuals transition from a walk to a run. Transitioning to a slow run rather than maintaining a fast walk at speeds near 2.0 m s^{-1} enhances metabolic efficiency by distributing more work to the spring-like ankle (Farris and Sawicki, 2012; Sawicki et al., 2009). We specifically instructed participants to maintain a walking gait and therefore do not have data for individuals running at 2.0 m s^{-1}; however, it would not be surprising to find that running reduces motor-like behavior and restores spring-like behavior of the ankle and its extensors (as is suggested by previously reported ankle joint power curves; Farris and Sawicki, 2012; Schache et al., 2015). Quantifying functional indices across a wider range of locomotor tasks (e.g. walking and running at the same speed) and establishing relationships between functional changes and locomotor performance (e.g. metabolic cost) are interesting and important avenues for future work.

Functional changes during uphill walking

In support of our second hypothesis, we observed decreased spring- and/or damper-like behavior and increased motor-like behavior at all three joints and their extensors during uphill walking. Specifically, as the slope got steeper, we observed decreased spring-like behavior at the hip and ankle and decreased damper-like behavior at the knee. Previous reports of decreased spring- and increased motor-like behavior of the human ankle during

accelerated compared with constant speed walking partially informed our hypothesis that local mechanical flexibility exists within the human locomotor system (Farris and Raiteri, 2017b; Qiao and Jindrich, 2016). We argue that quantifying mechanical functions during tasks that should, in theory, change functions in a specific direction would better test this hypothesis. Uphill and accelerated walking are mechanically similar in that both tasks require that net-positive work be done on the center of mass over each step. However, joint-level strategies used to meet this mechanical demand differ between the two tasks. During accelerated walking, net work at the hip and ankle become more positive while net work at the knee becomes more negative (Farris and Raiteri, 2017b; Qiao and Jindrich, 2016). Uphill walking, on the other hand, is associated with increased net-positive work at all three joints (Alexander et al., 2017). Additionally, at all three lower extremity joints, the magnitude of change in net work from level-ground to uphill walking appears to be far larger than the change that occurs from constant speed to accelerated walking (Alexander et al., 2017; Farris and Raiteri, 2017b; Qiao and Jindrich, 2016). For these reasons, we believed that the more mechanically challenging task of uphill walking offered a better method for testing the extent to which local mechanical flexibility is utilized within the human locomotor system. Our results confirmed this reasoning. In the current study, net work increased at the hip: (0.0 to 0.36 J kg^{-1}), knee (-0.03 to 0.14 J kg^{-1}) and ankle (0.07 to 0.48 J kg^{-1}) from 0 deg to +10 deg, confirming that our participants, on average, performed uphill walking with large increases in net-positive work at all three major lower extremity joints (Fig. 7). Accordingly, all three joints exhibited increased motor-like behavior. Future studies may further explore the extent of local mechanical flexibility within the human locomotor system by quantifying mechanical functions during other tasks that should require specific changes. For

example, downhill walking requires that net work be negative over each step, which likely results in decreased motor-like and increased damper-like function from the lower extremity joints and their major muscle groups (Franz et al., 2012).

Increased motor-like behavior in response to uphill locomotion is consistent with similar analyses conducted in other terrestrial animals. For example, increased motor-like behavior has been observed in turkeys, guinea fowl and goats during uphill running and walking (Arnold et al., 2013; Gabaldón et al., 2004; Higham et al., 2007). Thus, it is relatively unsurprising that humans incorporate the same local mechanical flexibility. Interestingly, slope-induced local mechanical flexibility does not appear to exist in all terrestrial animals. For example, distal muscles of tammar wallabies do not alter their mechanical function during incline versus level hopping (Biewener et al., 2004). Rather, the proximal muscles of these animals generate the work required to hop uphill, indicating that wallabies rely primarily on central rather than local mechanical flexibility (McGowan et al., 2007). Rather than alter each component within the locomotor system, these animals shift the mechanical workload to the locomotor components best suited to perform the functions required by the environment. Thus, there appear to be across species differences in slope-induced local mechanical flexibility similar to the speed-induced differences discussed above, both of which warrant further investigation. Our results, combined with those of previous studies, suggest that local mechanical flexibility is an important biomechanical feature of locomotion for humans and for many other (but not all) terrestrial animals.

Extending the functional indexing analysis to individual muscle groups

Although it was not our primary purpose, an important and novel aspect of this study was the extension of the functional indexing
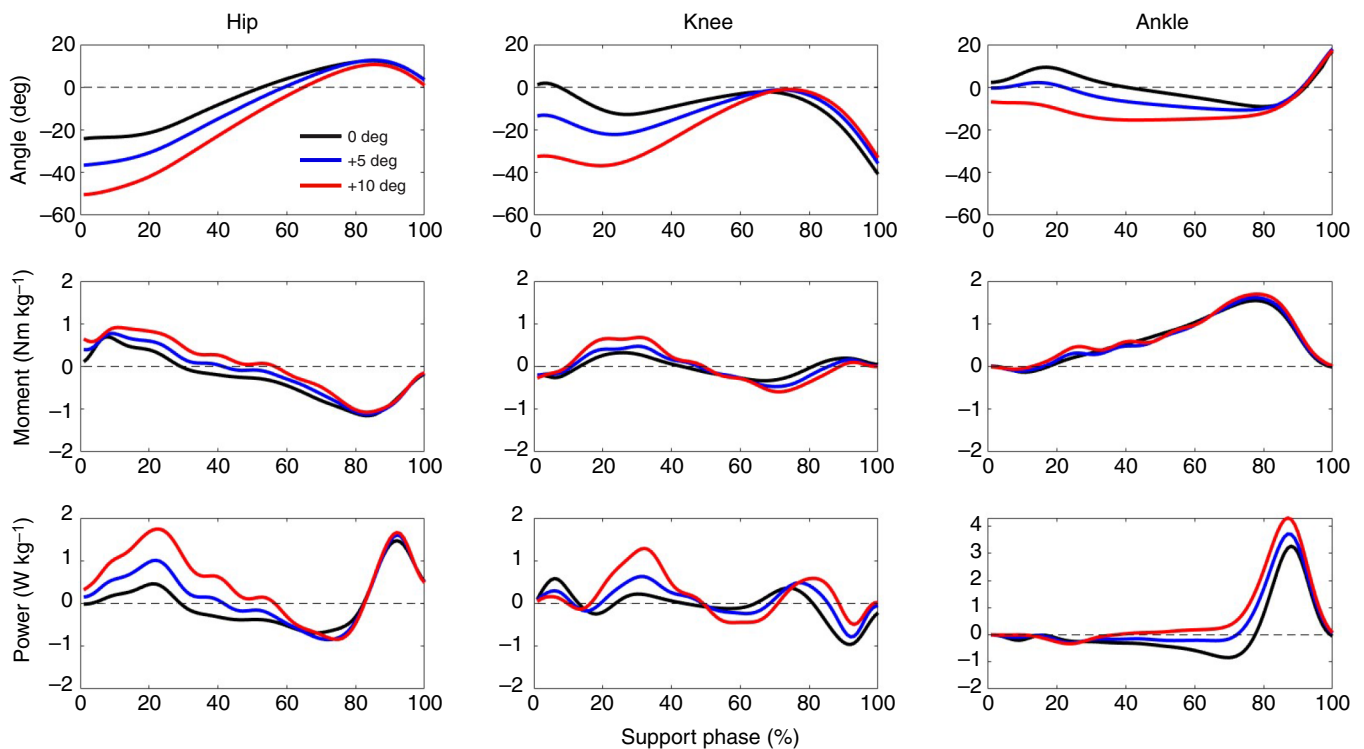

Fig. 7. Ensemble curves for hip, knee and ankle joint angles, moments and powers across all slopes. Group (*n*=13) data represent the support phase only and moments and powers were normalized to body mass. Participants walked at 1.2 m s^{-1} over 0 deg (black lines), +5 deg (blue lines) and +10 deg (red lines).

analysis from whole joints to individual muscle groups. This revealed several noteworthy observations. First, the flexor and extensor muscle groups at each joint rarely performed the same mechanical function (however, in rare instances, they did: both the extensors and the flexors of the knee acted as struts while walking at 1.2 m s^{-1} at +5 deg). This highlights the importance of quantifying functional indices at biological levels beyond whole joints. Second, functional changes at the whole joint appeared to be primarily driven by functional changes of the extensor muscle groups. An exception to this was mechanical function of the hip joint during level (but not uphill) walking, which appeared to be dictated more by the flexor muscles. The apparent importance of the extensors in governing joint-level function is perhaps unsurprising, given the large role of these muscles during human walking (e.g. providing bodyweight support and propelling the body upward and forward). Extending the functional indexing analysis from whole joints to muscle groups requires only one extra step – identifying onsets and offsets of extensor and flexor moments – and is thus relatively easy to incorporate into future analyses.

Potential consequences of reduced mechanical flexibility

Animals very often move through incredibly complex environments and to do so, rely on locomotor systems capable of flexibly altering internal mechanics to meet external demands. It is important to consider potential consequences of losing this mechanical flexibility. In the wild, the inability of an animal to effectively negotiate its environment could impair its ability to hunt or forage for food and leave it more vulnerable to predation (Bartholomew and Caswell, 1951; Dickinson et al., 2000; Schaeffer and Lindstedt, 2013; Zihlman, 1992). For humans, the consequences are perhaps less immediately life-threatening, but are nonetheless important. Even during normal, community ambulation through human-modified environments, individuals must often perform locomotor tasks with varying demands (e.g. walking uphill/downhill, ascending/descending stairs, avoiding obstacles, etc.) and thus require mechanical flexibility. Loss of mechanical flexibility might therefore limit community ambulation and lead to reduced overall quality of life. There are also potential consequences for locomotor capacity (e.g. speed, energetic cost, dynamic stability) in general. For example, advanced age is associated with decreased mechanical output from the ankle extensors and increased mechanical output from the hip extensors and/or flexors (DeVita and Hortobagyi, 2000; Franz and Kram, 2014; Kuhman et al., 2018b; Silder et al., 2008). Furthermore, the magnitude of this distal-to-proximal shift in joint-level mechanical output is larger during maximal compared with comfortable speed walking and during uphill compared with level-ground walking (Kuhman et al., 2018a,b; Waanders et al., 2018). It is possible that age-related biological changes to the extensors (e.g. loss of muscle strength, sub-tendon coupling in the Achilles) decrease the local flexibility of this muscle group, rendering it unable to 'adapt' to changing external demands and necessitating a central shift from the ankle to the hip (Franz and Thelen, 2015, 2016). It is unclear whether this mechanical redistribution with age is beneficial or detrimental for locomotor capacity, however some flexibility is likely better than none (Franz, 2016; Kuhman et al., 2018b). A worst-case scenario would be loss of both local and central mechanical flexibility, which would render an individual unable to adapt to environmental demands. Such a scenario might be the case in individuals with Parkinson's disease (Kuhman et al., 2018a). Future studies exploring the effects of advanced age, as well as disorders associated with gait dysfunction

(e.g. post-stroke, Parkinson's disease, multiple sclerosis, etc.), on both central and local mechanical flexibility are warranted to determine whether loss of such flexibility contributes to the dysfunction.

Limitations

Several limitations should be considered when interpreting these results. First, we quantified functional indices during the support phase only. Inclusion of the swing phase may alter functional indices (Farris and Raiteri, 2017b). For example, if positive work performed by the hip extensors during early support is immediately preceded by negative work during late swing, then analyzing support phase only may underestimate the spring index and overestimate the motor index of this muscle group, as some energy may be stored in late swing and returned in early support. Second, our muscle group analyses relied on joint-level moments estimated using inverse dynamics, which provide the net action across each joint and cannot completely isolate actions of individual muscle groups. This limited our ability to establish firm relationships between morphology and function. Combining the functional indexing method with musculoskeletal modelling, as was described recently, could provide a better test of local mechanical flexibility of individual MTUs and muscles (Lai et al., 2019). Third, the spring index is likely overestimated because the calculation assumes that all negative work proceeded immediately by positive work can be conserved passively. This is unrealistic in even highly efficient biological tissue (Zelik and Franz, 2017). Future work is warranted to address this shortcoming, perhaps by incorporating joint- or muscle-group-specific 'efficiency' terms that regulate the amount of work that could realistically be conserved (Whittington et al., 2008). Fourth, although this analysis quantifies mechanical function at each joint and muscle group, it does not take into account the amount of work performed at each joint or by each muscle group. For example, although we provide evidence that all three joints become more motor-like during uphill walking, total positive work is disproportionately increased at the hip compared with the knee or ankle during uphill walking (Alexander et al., 2017; Franz and Kram, 2014; Kuhman et al., 2018b; Lay et al., 2006). This suggests that, although all three joints and their extensors act more like motors during uphill walking, humans prefer to distribute most of the added work incurred from the task to a specific joint or muscle group (in the case of uphill walking, the hip extensors). This represents the potentially complex interaction between central and local mechanical flexibility within animal locomotor systems. Better statistical models may be able to address this issue in the future. Finally, our analysis was limited to sagittal plane mechanics. Although we referred to the flexors and extensors as the major muscle groups of the lower extremity, there are other important muscle groups whose mechanical functions were not quantified (Hurt and Grabiner, 2015).

Conclusion

Our results provide further support for the idea that major lower extremity joints and muscle groups within the human locomotor system can alter their function to meet the demands of the locomotor task being performed. This local mechanical flexibility compliments central flexibility, a gait feature already well-established in the human locomotor system. Combined, these two forms of mechanical flexibility provide humans – and many other terrestrial animals – with the capacity to move through complex natural and modified environments, which is a crucial component of survival.

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