RESEARCH ARTICLE

Modulation of joint and limb mechanical work in walk-to-run transition steps in humans

Neville J. Pires[1], Brendan S. Lay[1] and Jonas Rubenson[1,2,*]

ABSTRACT

Surprisingly little information exists of the mechanics in the steps initializing the walk-to-run transition (WRT) in humans. Here, we assess how mechanical work of the limbs (vertical and horizontal) and the individual joints (ankle, knee and hip) are modulated as humans transition from a preferred constant walking velocity (v_{walk}) to a variety of running velocities (v_{run}; ranging from a sprint to a velocity slower than v_{walk}). WRTs to fast v_{run} values occur nearly exclusively through positive horizontal limb work, satisfying the goal of forward acceleration. Contrary to our hypothesis, however, positive mechanical work remains above that at v_{walk} even when decelerating. In these WRTs to slow running, positive mechanical work is remarkably high and is comprised nearly exclusively of vertical limb work. Vertical-to-horizontal work modulation may represent an optimization for achieving minimal and maximal v_{run}, respectively, while fulfilling an apparent necessity for energy input when initiating WRTs. Net work of the WRT steps was more evenly distributed across the ankle, knee and hip joints than expected. Absolute positive mechanical work exhibited a clearer modulation towards hip-based work at high accelerations (>3 m s^{-2}), corroborating previous suggestions that the most proximal joints are preferentially recruited for locomotor tasks requiring high power and work production. In WRTs to very slow v_{run} values, high positive work is nevertheless done at the knee, indicating that modulation of joint work is not only dependent on the amount of work required but also the locomotor context.

KEY WORDS: Walk, Run, Gait transition, Joint work, Limb work

INTRODUCTION

Among the most universal locomotor patterns is the transition from walking to running to move faster. Many studies have investigated the biomechanical, physiological and/or psychological explanations for the spontaneous (self-selected) transition from walking to running in humans (WRT; Mercier et al., 1994; Hreljac, 1995; Mohler et al., 2007; Pires et al., 2014). These studies have generally involved constant-velocity locomotion and focused on the transition to running that occurs as walking velocity is increased beyond a threshold where walking is no longer the preferred gait. Although central to our understanding of human gait transition, these studies focused on WRT velocities ($\sim$2.0 m s^{-1}) that are generally avoided during normal locomotion. For example, it has been shown that, in towns and cities,

walking velocities range from approximately 0.75–1.8 m s^{-1} (Bornstein, 1979; Minetti et al., 1994). How these previous studies relate to the WRT that takes place from a slower, more natural, walking velocity is unclear. In many cases, the decision to transition from a walk to a run occurs not through an increase in walking velocity up until we experience discomfort, as has been the case in most WRT studies, but rather is achieved via a direct transition from slower, more comfortable walking. Surprisingly little data exists for the mechanics of the WRT from these typical habitual walking velocities. Further, relatively few studies have examined the mechanics of accelerating from walking to running during the actual transition steps themselves (although see Van Caekenberghe et al., 2010b; Segers et al., 2013). Thus, how the joints and limbs combine to achieve the WRT remains surprisingly poorly understood.

Studies assessing a range of constant-velocity walking and running indicate that the ankle is a key joint dictating the transition from fast walking to slow running (Neptune and Sasaki, 2005; Farris and Sawicki, 2011a,b; MacLeod et al., 2014; Pires et al., 2014). However, unlike constant-velocity analyses, WRT acceleration steps necessitate a net input of positive mechanical work and can thus be expected to have a distinct limb and joint mechanical pattern compared with both steady-velocity walking and running. Studies on humans indicate a greater reliance on proximal joints for net positive work production (Hubley and Wells, 1983; Roberts and Belliveau, 2005; Qiao and Jindrich, 2016). This shift in work distribution may be explained on the basis that long-fibered parallel muscles associated with the proximal joints have a greater capacity to perform mechanical work compared with the short-fibred pennate muscles of the distal limb (Biewener, 1998; Biewener and Roberts, 2000). Greater reliance on proximal joints to input high net positive work is nevertheless not universal. For example, turkeys performing bipedal running acceleration steps exhibit near equivalent net ankle and hip joint work across a range of acceleration levels (Roberts and Scales, 2004), and wallabies rely predominantly on net ankle work (McGowan et al., 2005). At a limb level, it has been demonstrated that as step acceleration increases in turkeys, negative work drops to zero such that net work is represented solely by positive work production (Roberts and Scales, 2002). In this study, the ratio of peak horizontal to vertical force increased substantially at higher accelerations. These results suggest that increasing acceleration may also be achieved through modulating the ratio of horizontal to vertical work. The details of how limb and joint work is modulated across WRT accelerations is not known for human gait.

The purpose of this study was to assess how mechanical work at the limbs (both horizontal and vertical work) and individual joints (ankle, knee and hip) is modulated as humans transition from a preferred walking velocity (v_{walk}) to a variety of running velocities (v_{run}; ranging from a sprint to a running velocity that is slower than v_{walk}). While transitioning to v_{run} slower than v_{walk} is unnatural, and unlikely to occur under normal conditions, they are included to help

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List of symbols and abbreviations

C_H, C_V	horizontal and vertical integration constants
COM	center of mass
F_H, F_V, F_{ML}	horizontal, vertical and medio-lateral GRF acting on the limb
g	gravitational constant (9.81 m s^{-2})
GRF	ground reaction force
m	body mass
P_H, P_V, P_{tot}	horizontal, vertical and total limb power
S1	Step 1
S2	Step 2
v_H, v_V, v_{ML}	horizontal, vertical and medio-lateral center of mass velocity
v_{run}	running velocity
v_{walk}	preferred walking velocity
W_H^{net}, W_H^+, W_H^-	net, positive and negative horizontal limb work
W_V^{net}, W_V^+, W_V^-	net, positive and negative vertical limb work
W_{tot}^{net}, W_{tot}^+, W_{tot}^-	net, positive and negative total limb work
WRT	walk-to-run transition

reveal more comprehensively the fundamental biomechanical control paradigms of the WRT. We have chosen to investigate both the net mechanical work at the limbs and joints as well as the absolute positive (and negative) work. In net work calculations, energy absorption and generation across the step cancel and thus they represent the overall effect that the specific limb or joint has on accelerating the center of mass (COM) between the start and end of the step. Absolute work captures the cumulative amount of positive (and negative) work that the joint delivers to the COM within the step. Partitioning absolute positive and negative work is important for understanding how the limb and joints accelerate the COM in cyclical movements that include periods of energy absorption and generation, where examining net work alone might obscure their role (Sasaki et al., 2009). Finally, partitioning the amount of work performed to accelerate the COM vertically versus horizontally further helps explain the functions of the limbs and individual joints across WRTs ranging from low to high acceleration.

We first hypothesized that, at the highest WRT accelerations, net work would be generated exclusively through positive mechanical work. We also hypothesized that positive work will decrease below the value at v_{walk} when decelerating into a run and start to approach zero, because an input of work is theoretically no longer a mechanical requirement. These predictions were based, in part, on data from fast-accelerating turkeys (Roberts and Scales, 2002, 2004) that provide among the most comprehensive data on bipedal acceleration steps. Secondly, we hypothesized that a greater reliance on mechanical work production at the proximal joints (knee and hip) and a reduced reliance on work at the distal joint (ankle) occurs with increasing WRT accelerations, similar to that observed in other human locomotor tasks when the requirement for positive mechanical work is high (Hubley and Wells, 1983; Roberts and Belliveau, 2005; Farris and Raiteri, 2017).

MATERIALS AND METHODS
Participants
Ten healthy and recreationally active male participants with no history of major lower-limb injury were recruited for this study (age: 26.3±2.4 years; height: 174.9±6.8 cm; mass: 74.3±13.7 kg; means± s.d.). Previous work indicated that this sample size is suitable for detecting velocity-dependent effects on joint mechanics (Pires et al., 2014). All testing procedures were approved by the Human Research

Ethics Committee of the University of Western Australia. Written informed consent was obtained from all participants.

Walk-to-run conditions
Prior to conducting gait transition trials, the participants' average self-selected (preferred) walking velocity (v_{walk}) was determined by having the participants walk 20 m through a gait laboratory (the velocity calculations are described in further detail below and in Fig. 1). Participants were subsequently instructed to change from their v_{walk} to one of five running velocities (referred to as v_{run}): (1) a v_{run} that was slower than their v_{walk}, (2) a v_{run} that was the same as their v_{walk}, (3) a jog, (4) a fast run and (5) a sprint. The five v_{run} transitions were repeated a minimum of five times and performed in random order to avoid order effects. The participants were instructed to initiate the transition so that their first transition step (referred to as S1) occurred on one force plate (2000 Hz; 9261A Kistler, 0.6×0.4 m Winterthur, Switzerland) and their subsequent step (referred to as S2) occurred on a second force plate (2000 Hz; BP12001200-4K AMTI 1.2 m×1.2 m, Watertown, MA, USA). The participants could choose whichever leg felt comfortable to initiate the transition step. They were instructed to maintain their v_{walk} prior to the transition step, irrespective of the instructed transition velocity. If the walking velocity leading up to the transition steps did not match within 0.3 m s^{-1} of their v_{walk}, the trials were repeated.

We conducted a secondary test where our participants were instructed to change from their v_{walk} to either (1) a walk faster than their v_{walk} or (2) a walk slower than their v_{walk}.
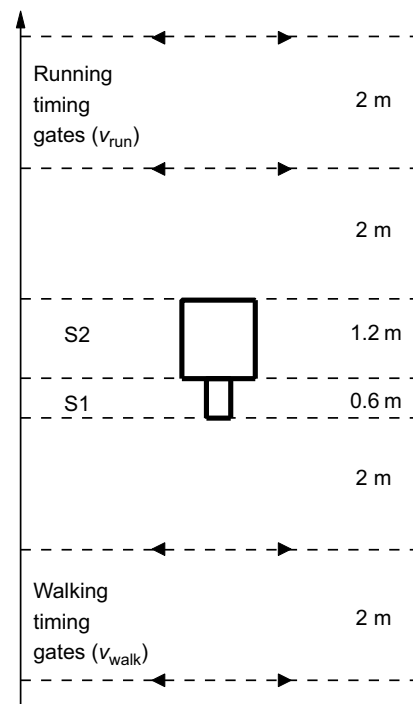

Fig. 1. Diagram of the laboratory set up. The preferred walking velocity (v_{walk}) was measured from timing gates separated by 2 m and placed 2 m in front of the first force plate. The first (S1) and second (S2) transition step velocities were measured from markers placed on the participant's pelvis. S1 occurred on the first force plate [0.6 m (in the direction of motion) by 0.4 m]. S2 occurred on the second force plate (1.2 by 1.2 m). The final velocity (v_{run}) was measured from timing gates separated by 2 m and placed 2 m after the second force plate.

Velocity and acceleration measurements

The v_{walk} of the participants as they approached the transition step was measured by a set of timing gates placed 2 m in front of the first force plate. v_{run} was measured by a second set of timing gates placed 2 m after the second force-plate (Fig. 1). The v_{run} reported in this study is thus the running velocity that was achieved after the two recorded transition steps and not the velocity across these transition steps themselves. The average acceleration and velocity across the individual gait transition steps (S1 and S2) were computed by the mean horizontal acceleration and velocity of the mid-pelvis over the stance phase (heel strike to toe-off) of each respective step. As there was still a double support phase during S1, we were unable to calculate the COM acceleration and velocity of the complete S1 step using the ground reaction force (GRF) method (Donelan et al., 2002) as we did not have a force plate to measure the GRF of the contralateral foot during the double support phase. We did, however, compare the average pelvis linear horizontal acceleration with the acceleration calculated from numerical integration of the GRF of S2 when no double support was present (Donelan et al., 2002; see below for a detailed description of methodology). The average pelvis linear horizontal acceleration was found to be systematically slightly greater than the acceleration calculated from the GRF, but the two methods were strongly correlated (r^2=0.92 for the acceleration; Fig. 2A). This difference resulted in slightly different slopes of mechanical work versus acceleration compared with using the GRF-derived acceleration, but did not alter the conclusions of the study.

Three-dimensional gait analysis and joint mechanics

For a detailed description of the three-dimensional (3D) gait analysis, joint moments and power calculations, please refer to Pires et al., (2014). Briefly, 3D GRFs (2000 Hz) and marker position data (250 Hz; 10 camera VICON MX motion analysis system; VICON Oxford Metrics, Oxford, UK) were captured whilst participants transitioned from walking to running. Prior to inverse dynamic modeling, marker position data and the GRFs were filtered using a fourth-order, 8 Hz low-pass Butterworth filter (filter frequency was selected by performing a residual analysis of filtered versus unfiltered data). Three-dimensional kinematic and inverse dynamic calculations were computed in Vicon Nexus and Bodybuilder software (VICON, Oxford Metrics, Oxford, UK) in accordance with Besier et al. (2003) and outlined in more detail in Pires et al. (2014).

Joint work calculations have also been previously detailed in Pires et al. (2014). Briefly, the net joint work for S1 and S2 were calculated from the time integral of the joint power curves, respectively, over the stance phase. Positive and negative joint work for S1 and S2 were calculated from the time integral of the positive and negative values of the joint power curves, respectively, over the stance phase.

Total joint powers for S1 and S2 were calculated by summing the instantaneous power traces at each joint. Net total joint mechanical work for S1 and S2 were calculated by integrating the values of the total joint power trace with respect to time. Positive and negative total joint mechanical work for S1 and S2 were calculated by integrating the positive and negative values of the total joint power trace with respect to time.

Limb mechanical work

The net, positive and negative horizontal ($W_{\text{H}}^{\text{net}}$, W_{H}^{+}, W_{H}^{-}), vertical ($W_{\text{V}}^{\text{net}}$, W_{V}^{+}, W_{V}^{-}) and total ($W_{\text{tot}}^{\text{net}}$, W_{tot}^{+}, W_{tot}^{-}) mechanical work performed by each limb over the stance phase were calculated using the 'individual limb method' outlined by Donelan et al. (2002). The mechanical power produced by each lower limb in the horizontal (P_{H}) and vertical (P_{V}) directions were computed as the dot product
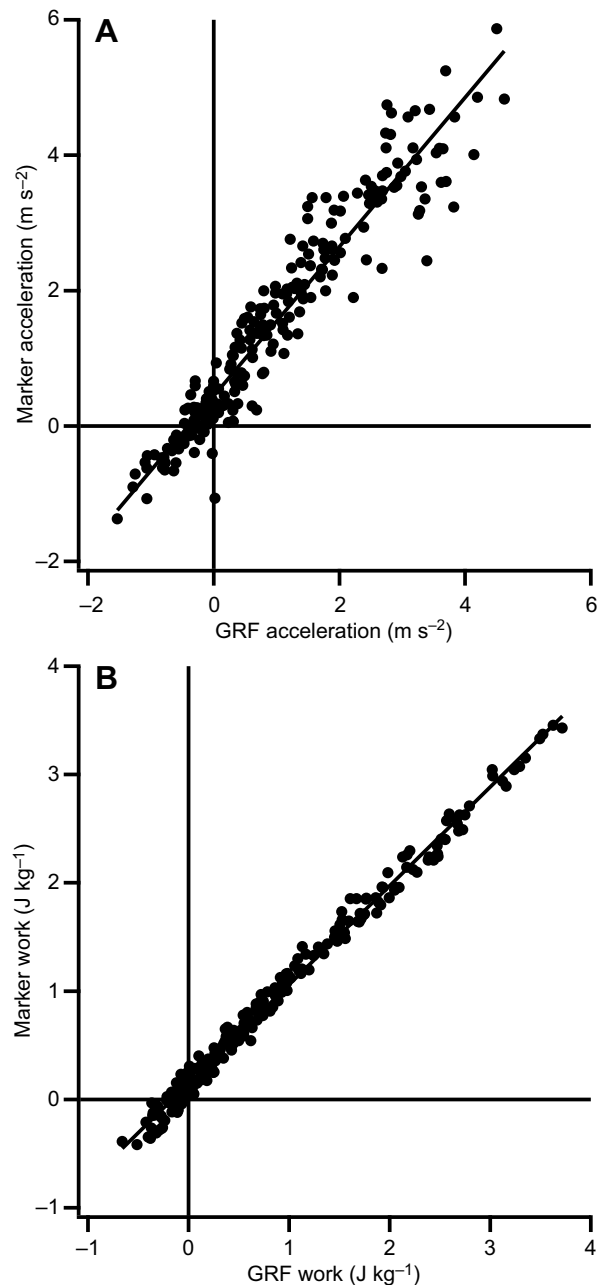

Fig. 2. Comparison between marker- and GRF-derived acceleration and work. (A) Regression of the center of mass (COM) acceleration calculated from the ground reaction force (GRF) and the acceleration estimated from motion capture of markers placed on the participant's (N=10) pelvis (line of best fit equation: a_{mkr}=1.10·a_{GRF}+0.44; r^2=0.92). (B) Regression of net mechanical limb work in S2 calculated from the GRF approach (see Materials and Methods) and the net mechanical limb work in S2 computed using the estimated COM velocity from markers placed on the participant's pelvis (line of best fit equation: W_{mkr}=0.91·W_{GRF}+0.15; r^2=0.99).

of the horizontal and vertical external force acting on the limb (F_{H}, F_{V}) and the horizontal and vertical velocity of the COM (v_{H}, v_{V}), respectively:

$$P_{\text{H}} = F_{\text{H}} \cdot v_{\text{H}} \tag{1}$$

and

$$P_{\text{V}} = F_{\text{V}} \cdot v_{\text{V}}. \tag{2}$$

The total limb power generated on the body's COM was computed from the sum of the horizontal, vertical and medio-lateral power:

$$P_{tot} = F_H v_H + F_V v_V + F_{ML} v_{ML}, \qquad (3)$$

where F_{ML} and v_{ML} are the medio-lateral GRF and COM velocity, respectively. The COM velocities in each direction were estimated from the motion of the mid-pelvis measured using our motion capture system. Medio-lateral work was small and was not specifically assessed further in subsequent analyses. Net horizontal, net vertical and net total limb mechanical work were computed by integrating limb power over the stance phase:

$$W_H^{net} = \int_{t_i}^{t_f} P_H \, dt, \qquad (4)$$

$$W_V^{net} = \int_{t_i}^{t_f} P_V \, dt, \qquad (5)$$

$$W_{tot}^{net} = \int_{t_i}^{t_f} P_{tot} \, dt, \qquad (6)$$

where t_f is foot off, t_i is foot strike and dt is stance time.

Positive and negative horizontal, vertical and total limb mechanical work were computed by integrating limb power and restricting to positive and negative values, respectively:

$$W_H^+ = \int_{t_i}^{t_f} P_H^+ \, dt, \quad W_H^- = \int_{t_i}^{t_f} P_H^- \, dt, \qquad (7)$$

$$W_V^+ = \int_{t_i}^{t_f} P_V^+ \, dt, \quad W_V^- = \int_{t_i}^{t_f} P_V^- \, dt, \qquad (8)$$

$$W_{tot}^+ = \int_{t_i}^{t_f} P_{tot}^+ \, dt, \quad W_{tot}^- = \int_{t_i}^{t_f} P_{tot}^- \, dt. \qquad (9)$$

For S2, in which the entire stance phase is in single support, we assessed how the limb work calculated using the pelvis velocity compared with limb work calculated using a COM velocity derived from force plate recordings. For this comparison, the COM velocities in each direction were calculated by integrating the acceleration of the COM with respect to time. Horizontal and vertical COM accelerations were derived from the components of the GRF and by the participants' body mass (and incorporating the acceleration due to gravity in the vertical direction):

$$v_H = \int_{t_i}^{t_f} \frac{F_H}{m} \, dt + C_H, \qquad (10)$$

$$v_V = \int_{t_i}^{t_f} \frac{F_V - m\boldsymbol{g}}{m} \, dt + C_V, \qquad (11)$$

where m is the body mass of the participants, $\boldsymbol{g}$ is the gravitational acceleration (9.81 m s^{-2}), and C_H and C_V are integration constants. The integration constants were calculated as the difference between the average velocity (horizontal and vertical: $\bar{v}_H$, $\bar{v}_V$) of the pelvis and the average horizontal and vertical velocity calculated from the

numerical integration of the GRF across the stance phase. The remainder of the work calculations were the same as those of Eqns 1–9. The mechanical work calculation using the two separate methods for S2 resulted in only very small differences that did not alter conclusions drawn in this study (Fig. 2B).

Statistics

In post-testing, the recorded v_{run} from the second timing gates were grouped as follows: (1) <1.5 m s^{-1}; (2) 1.5 m s^{-1}<v_{run}<2.5 m s^{-1}; (3) 2.5 m s^{-1}<v_{run}<3.5 m s^{-1}; (4) 3.5 m s^{-1}<v_{run}<4.5 m s^{-1}; and (5) >4.5 m s^{-1}. Within these groups a one-way repeated measures ANOVA (post hoc comparison with Bonferroni correction and a significance level of $P<0.05$) was used to compare velocity between v_{walk}, the average velocity of S1 and S2, and v_{run}.

The limb and joint work measures of S1 and S2 for each participant were plotted against the average COM acceleration of each step. We determined whether a linear or curvilinear regression line best fit each participant's limb and joint work versus acceleration data by increasing the order of the polynomial until the highest coefficient was no longer significantly different from 0. At this point, increasing the number of coefficients did not improve the fit of the data.

To assess the relationships between limb and joint work measures and acceleration, we first computed the work in both S1 and S2 at accelerations common to all participants (−1.0, 0, 1.0, 2.0, 3.0, 4.0 and 5.0 m s^{-2}) using the participant-specific regression equations described above. Using these calculated values, we performed one-way repeated measures (seven acceleration levels) ANOVAs on S1 and S2 limb work measures at a P-level of <0.05. We also performed a two-way (joint: ankle, knee and hip) by seven repeated measures ANOVA (seven acceleration levels) at a significance level of $P<0.05$ for both S1 and S2 to assess how net, positive and negative joint work was modulated across acceleration. The same ANOVA was run on the percent contribution that each individual joint had to the summed net, positive and negative joint work, after performing an arc-sine transformation. Post hoc comparisons with Bonferroni corrections were used to determine significant differences between individual joints. If an interaction effect between joint and acceleration was present, we tested for significance between percent work contribution in individual joints at each acceleration; we used a paired-sample Student's t-test on arc-sine transformed data with Bonferroni corrections for multiple comparisons. A paired-sample Student's t-test was used to determine whether there was a significant difference between the total joint work performed in WRT accelerations versus that generated when the same acceleration was achieved by walking faster/slower.

RESULTS
Step velocity

In the first step of the WRT (S1), irrespective of the instructed running velocity condition, our participants increased their horizontal velocity ($P<0.05$; Fig. 3). When instructed to transition to a run that was slower than their v_{walk}, our participants increased horizontal velocity, but decelerated thereafter (Fig. 3A). Except for transitioning from walking to an instructed run that was intended to be the same velocity as the v_{walk} (~1.5 m s^{-1}), our participants were not able to achieve a constant velocity between S2 and the final v_{run} (Fig. 3B). When transitioning to running velocities that were greater than 2.5 m s^{-1} (instructed 'fast runs' and 'sprints'), our participants' horizontal velocity increased between all steps (Fig. 3C–E).
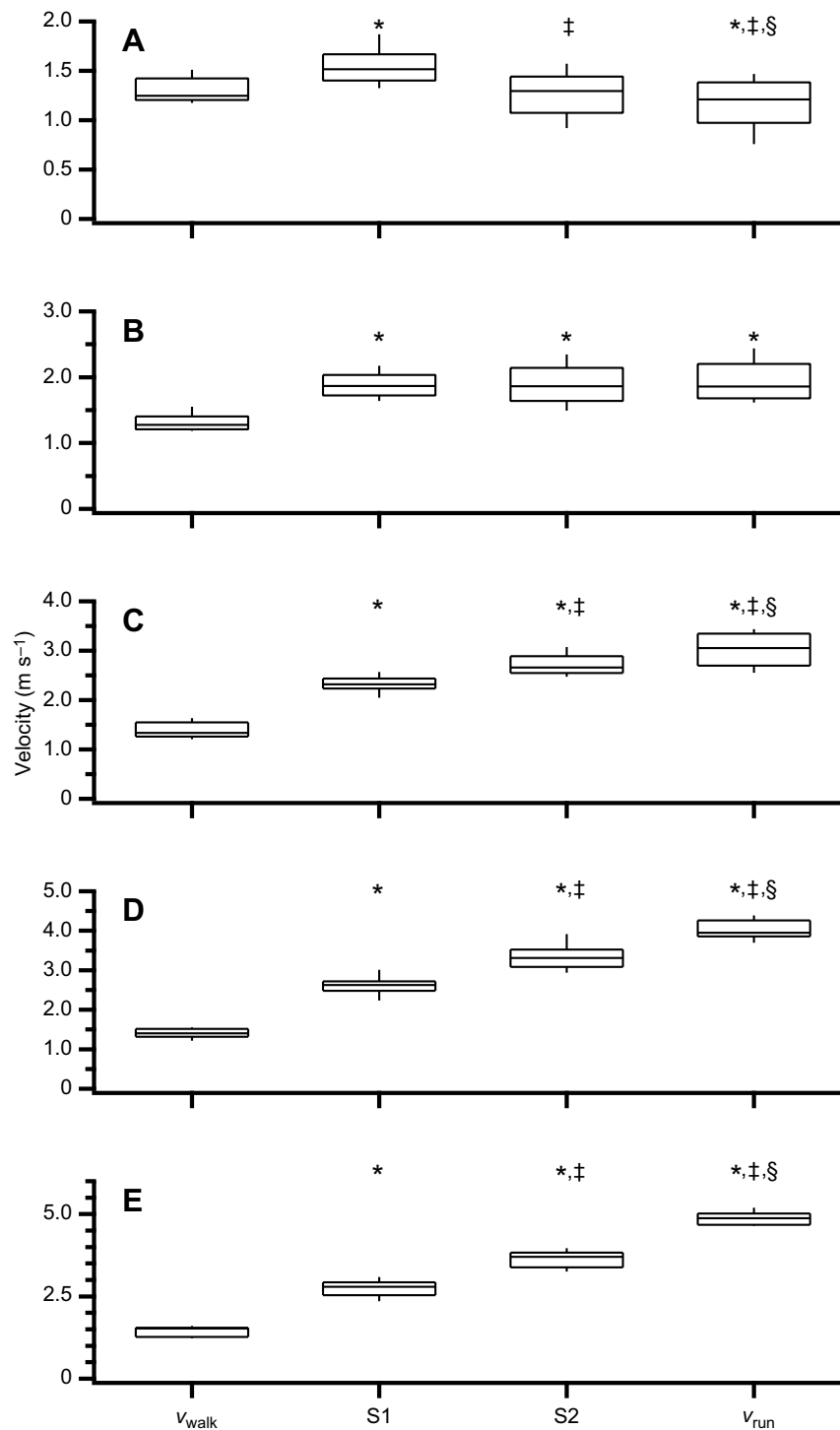
Fig. 3. Box and whisker plots of the preferred walking velocity (v_{walk}), S1 and S2 transition step velocity, and the final running velocity (v_{run}). Data have been grouped by the following v_{run} ranges: (A) <1.5 m s^{-1}; (B) 1.5 m s^{-1}<v_{run}<2.5 m s^{-1}; (C) 2.5 m s^{-1}<v_{run}<3.5 m s^{-1}; (D) 3.5 m s^{-1}<v_{run}<4.5 m s^{-1}; and (E) >4.5 m s^{-1}. Velocities were measured at the start of the walkway (v_{walk}); the first step where they transitioned to a running gait over the force plate (S1); the second transition step over the second force plate (S2); and the end of the walkway as the participants ran (v_{run}). v_{walk} and v_{run} were measured from timing gates placed 2 m either side of the force plates. The S1 and S2 velocities were measured from the average pelvis linear velocity measured over the stance phase for the respective step. Bonferroni *post hoc* adjustment was used to identify significant differences between the respective steps: *$P<0.05$ between v_{walk} versus S1, v_{walk} versus S2 and v_{walk} versus v_{run}; ‡$P<0.05$ between S1 versus S2 and S1 versus v_{run}; §$P<0.05$ between S2 and v_{run}.

Mechanical power

Example traces of the instantaneous ankle, knee and hip joint and total joint power plotted against the percentage of the stance phase for S1 and S2 are presented in Fig. 4. Owing to the quantity and spread of data, individual traces were chosen that corresponded to a v_{run} of 1.0, 3.0 and 5.0 m s^{-1}. The participant's self-selected constant-velocity running trial (~3.4 m s^{-1}) is also included (Fig. 4).

Vertical, horizontal and total limb work versus acceleration

There was a significant main effect of acceleration on all limb work measures for both S1 and S2, except for the vertical net work in S2

($P<0.05$; Fig. 5). As expected, the net total limb work increased with acceleration, but only became negative with a negative horizontal acceleration in S2 (Fig. 5E,F). Total negative limb work reduced to near zero at accelerations above ~3 m s^{-2} in S1 and 4 m s^{-2} in S2. Net work at these higher accelerations was therefore composed nearly exclusively of positive limb work. Positive total limb work increased with acceleration in S1 and S2, and was always above the positive work of v_{walk}. The positive and net horizontal mechanical work in both S1 and S2 significantly increased as step acceleration increased (Fig. 5A,B). At accelerations above 3–4 m s^{-2}, net horizontal work resulted purely from positive horizontal work
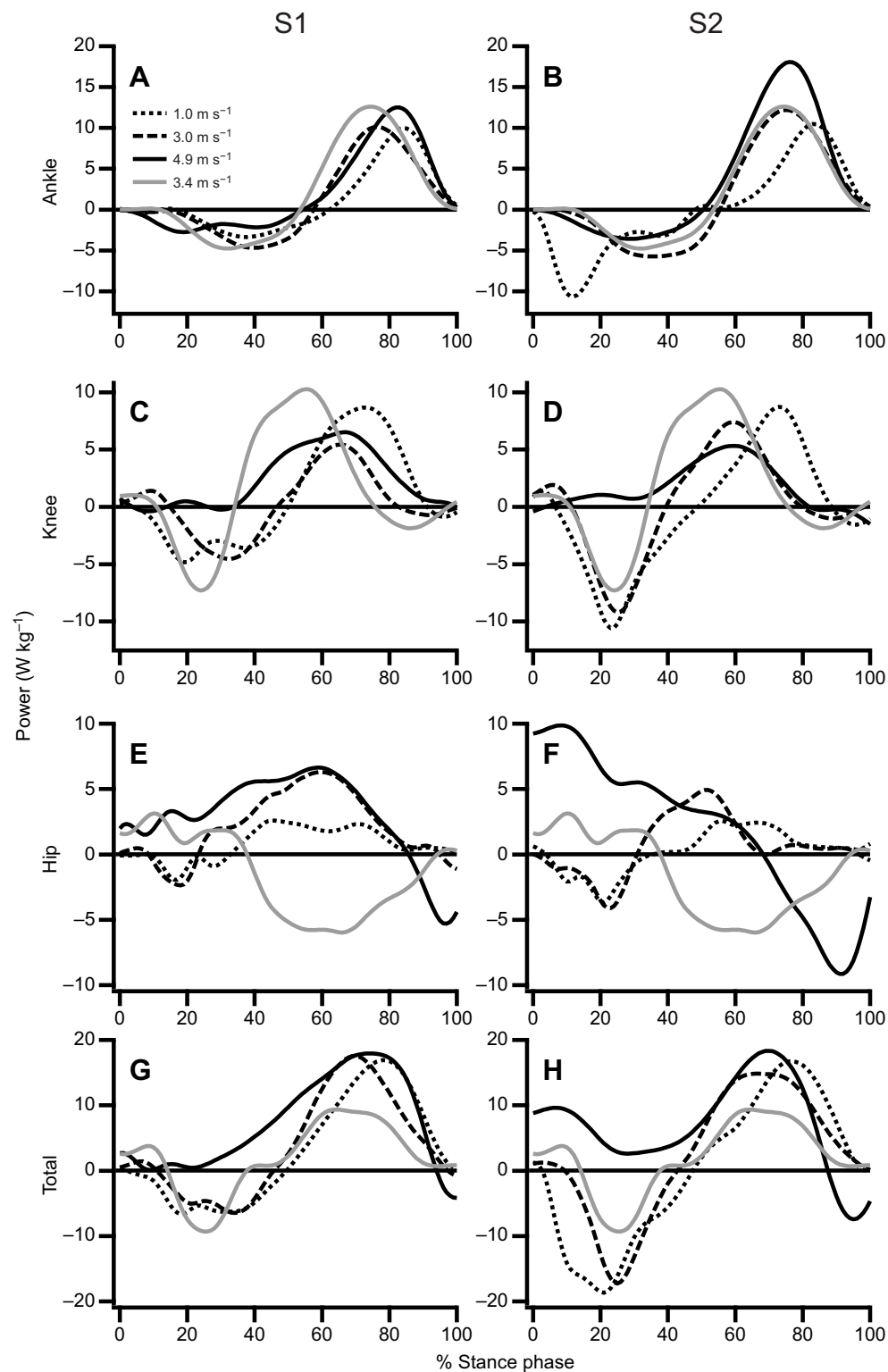
Fig. 4. Representative traces for the instantaneous ankle, knee, hip and total joint powers (body-mass normalized) for S1 and S2 plotted against the percent of the stance phase. Ankle (A,B), knee (C,D), hip (E,F) and total (G,H) powers are shown. The fine dotted line represents a WRT to a v_{run} of 1.0 m s^{-1}; the course broken line represents a WRT to a v_{run} of 3.0 m s^{-1}; and the solid black line represents a WRT to a v_{run} of 4.9 m s^{-1}. The solid grey line is an example trace of the joint power where the participant is running at a constant velocity of 3.4 m s^{-1} (self-selected running velocity).

production. Conversely, the net (S1) and positive (S1 and S2) vertical mechanical work significantly decreased as step acceleration increased (Fig. 5C,D; $P<0.05$).

Mechanical joint work versus acceleration
A full description of the ANOVA results for net, positive and negative joint work are presented in Table 1. A main effect of acceleration was observed across the joints (ankle, knee and hip) for

net, positive and negative joint work ($P<0.05$; net and positive work increased with increasing acceleration, whereas negative work decreased; Figs 6 and 7).

A main effect of joint was observed on net work in S1 and S2. *Post hoc* tests failed to identify any significant differences in net work between specific joints in S1. When the main effect of acceleration across joints was investigated further, *post hoc* tests revealed that the ankle net work was statistically greater than the
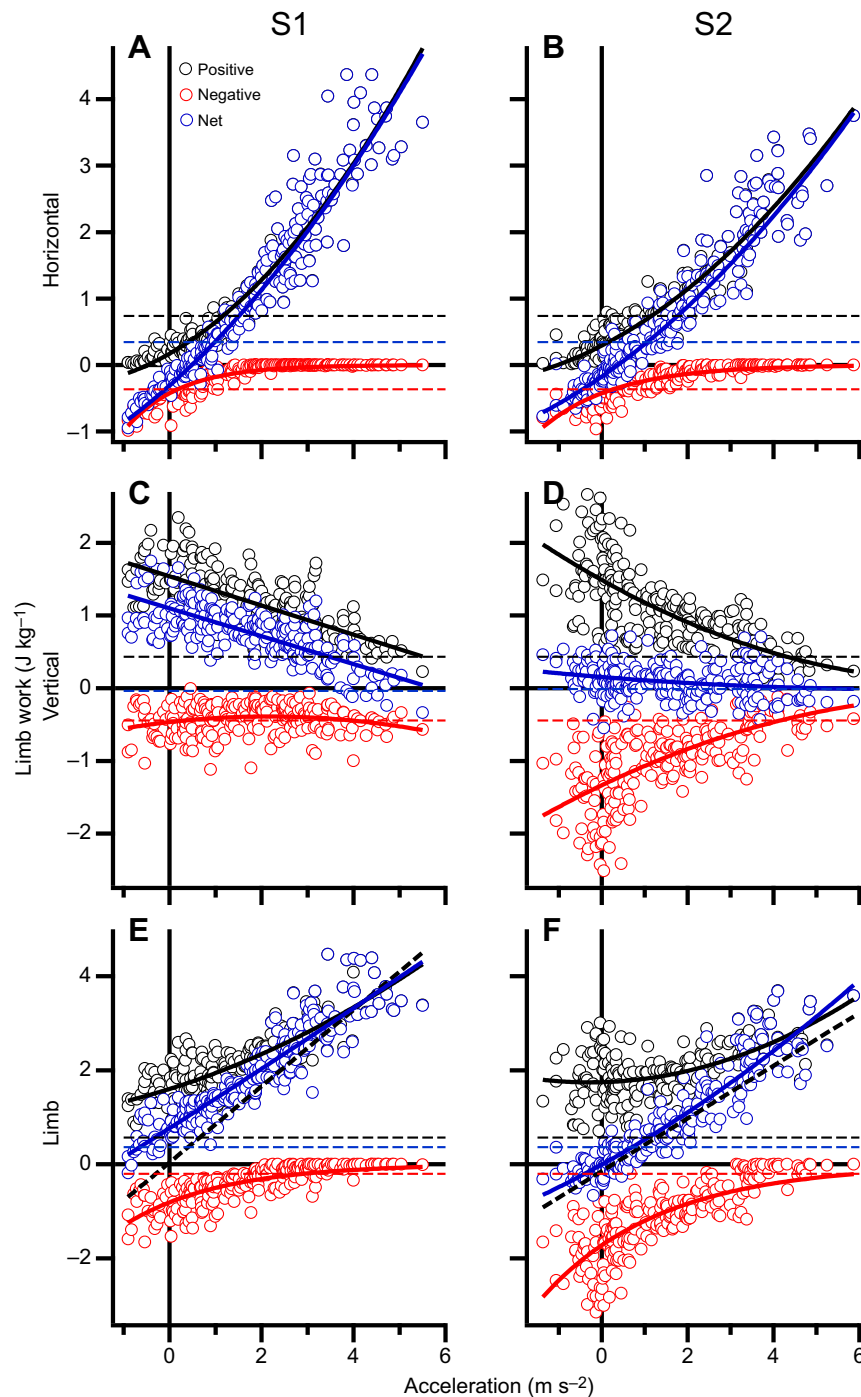
Fig. 5. Positive, negative and net body-mass-specific mechanical limb work in S1 and S2 for each participant (n=10) versus acceleration. Horizontal (A,B), vertical (C,D) and total (E,F) limb work. Solid colored lines are lines of best fit. The horizontal broken black, red and blue lines represent the positive, negative and net mechanical limb work performed during v_{walk} over one step, respectively. The thick dashed black line (E,F) represents the work required to accelerate the COM horizontally, calculated from the change in kinetic energy from the start to the end of the step.

knee and hip in S2 ($P<0.05$; Figs 6 and 7F). An interaction effect on net work was observed between joint and acceleration in S1 ($P<0.05$; Fig. 7F). *Post hoc* tests on percent net work in S1 showed that the ankle generates significantly more net work at low accelerations, whereas the hip generates more work at high accelerations ($P<0.05$; Figs 7E and 8E).

A main effect of joint was also observed on positive work in both S1 and S2. *Post hoc* tests found that positive work at the ankle was greater than the knee in S1, and was greater than the knee and hip in S2 ($P<0.05$; Table 1, Figs 6 and 7A,B). An interaction effect on positive work was observed between joint and acceleration in both S1 and S2 ($P<0.05$; Fig. 7A,B). *Post hoc* tests on percent positive work showed that the ankle and knee generate significantly more positive

work than the hip at low accelerations but that the hip increases its relative contribution to positive work at high accelerations ($P<0.05$; Figs 7A,B and 8A,B). In S1, the hip generates the most positive work out of all joints ($P<0.05$; Figs 7A and 8A).

Apart from the positive work done by the hip joint during both steps (Fig. 6E,F), the positive mechanical work of each joint during the transition step was always greater than that of the positive mechanical work of the joint when walking at the v_{walk} (horizontal dashed lines in Fig. 6).

We did not make any specific hypotheses regarding the relative amount of negative work among joints. We did observe significant main effects of joint on negative work and interaction effects between joints and acceleration in both S1 and S2. In summary,

Table 1. Joint work versus acceleration statistics

| | S1 | | | | | | S2 | | | | | |
| | Two-way ANOVA | | | Bonferroni | | | Two-way ANOVA | | | Bonferroni | | |
	Joint	Accel.	Int.	Ankle vs knee	Ankle vs hip	Knee vs hip	Joint	Accel.	Int.	Ankle vs knee	Ankle vs hip	Knee vs hip
Positive	**0.009**	**<0.001**	**<0.001**	**0.039**	1.00	0.074	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1.00
Negative	**<0.001**	**<0.001**	**<0.001**	0.950	**0.001**	**0.009**	**0.008**	**<0.001**	**<0.001**	0.967	**0.001**	0.139
Net	**0.017**	**<0.001**	**<0.001**	0.237	0.661	0.057	**<0.001**	**<0.001**	0.926	**0.002**	**0.001**	0.190

P-values indicating ANOVA main effects of joint and acceleration (Accel.) and their interaction effect (Int.). Bonferroni *post hoc* tests identify statistical differences between individual joints. Bold numbers signify statistical differences (*P*<0.05). For statistical differences between joints at specific levels of acceleration, please refer to Fig. 8.

when negative work production is largest (during low and negative horizontal accelerations) most negative work is produced at the knee (*P*<0.05; Figs 6 and 7C,D). Negative joint work is very small at high acceleration, but that which is produced is primarily in the ankle and hip (*P*<0.05; Figs 6 and 7C,D). A full description of the ANOVA results for negative work are presented in Table 1.

The positive, negative and net work required to both accelerate (0.49 ± 0.32 m s^{-2}) and decelerate (-0.47 ± 0.15 m s^{-2}) from the v_walk to faster/slower walking speeds was significantly less than the work required to transition to a run with an equivalent acceleration (*P*<0.05; Fig. 9).

DISCUSSION
General mechanical response to walk-to-run transition tasks
This study investigated limb and joint mechanics and their modulation during the transition from a preferred walking velocity to various targeted running velocities. The response to the instructed WRT was consistent across participants yet showed several unexpected features. First, we showed that humans have difficulty transitioning directly to a running gait that has a forward velocity equal to or slower than their preferred walking velocity (Fig. 3A,B). It is possible that the ability to directly decelerate from a walk to a very slow run is improved with practice. The challenge of decelerating into a slow run is supported by a total joint power profile that predominantly generates power, irrespective of whether the locomotor goal is to decelerate (Fig. 4G). Deceleration into a very slow run is instead primarily achieved in S2, after many of the participants had already transitioned to a run with an initial increase in forward velocity (Fig. 3A).

We also found that, when instructed to transition to a running gait with 'jogging' through to 'sprinting' velocities, a constant velocity is not achieved by the second (S2) step of the WRT (Figs 3, 6). Our analyses were limited to two steps and we cannot establish how many steps are required to achieve a constant forward velocity. Despite the inability of the participant to adhere strictly to the instructed transition tasks, a systematic response of the joints and limbs to a WRT spanning a broad range of running velocities and accelerations was observed.

Limb mechanical work as a function of the walk-to-run transition acceleration
In both S1 and S2, negative limb work (and negative total joint work) drops to zero as WRT acceleration increases (Figs 5, 6), supporting our hypothesis that humans, similar to avian bipeds, use purely positive mechanical work to achieve high forward acceleration. We also discovered that, in these high forward accelerations, humans generate nearly exclusive positive horizontal work. Together, these data show that humans generate work effectively when the goal is to accelerate the COM in the forward direction. Had negative work been

generated in high-acceleration steps, more positive work would be required to achieve the same net positive work. Likewise, if a greater portion of this work was directed in the vertical direction, more overall work would be required to generate the same horizontal work, and thus forward acceleration. Both these strategies theoretically minimize the muscle work required for high WRT accelerations. One way to gauge the effectiveness of the limb in accelerating the COM forward is to compare it to the theoretical mechanical work required to achieve the observed horizontal acceleration. This can be computed as $(1/2mv_{H_f}^2) - (1/2mv_{H_i}^2)$, where $v_{H_f}^2$ and $v_{H_i}^2$ are the final and initial velocities of the COM during the WRT step, respectively. The theoretical horizontal work confirms that, at high WRT accelerations, the limb (and presumably muscles) produces work that is indeed devoted nearly purely to the task of forward acceleration; nearly no mechanical work is 'wasted' in COM deceleration or vertical acceleration (Fig. 5).

Contrary to our hypothesis, however, positive limb (and positive total joint work) was always above that during steady-velocity walking, irrespective of the WRT acceleration. WRTs to very slow velocities incur remarkably high positive work considering the goal is to decelerate, not accelerate, the COM. WRTs to slow RUN velocities are consequently also associated with a large increase in negative work. This is necessary to generate the net negative horizontal work (Fig. 5A,B) required for reducing the forward speed of the COM. It is noteworthy that, even though some participants could reduce their forward velocity in S1, no participants were able to do so with an overall reduction in net limb work (Fig. 5E), raising the question of whether an input of energy is a fundamental control paradigm of transitioning from walking to running.

The high mechanical cost of transitioning to very slow running velocities results nearly completely from the generation of positive vertical limb work (Fig. 5). Although producing additional mechanical work is undesirable, if an initial input of energy is indeed a constraint on the WRT then directing this energy in the vertical direction is the best way to minimize unwanted forward acceleration. This is because an input of vertical work will have a minimal effect on forward velocity. It has been previously reported that, when participants are freely allowed to transition from a walk to a run, there is a large increase in velocity (referred to as a velocity jump) during the transition step (Van Caekenberghe et al., 2010a,b; Segers et al., 2013). Our results indicate that this velocity jump is still present at slow velocities but, rather than occurring horizontally, it occurs vertically. The second step in the WRT (S2) showed the most pronounced increase in positive limb work in WRTs involving a reduction in forward velocity. In these transitions it is remarkable that positive limb work is nearly equivalent to that of transitioning from a walk to a sprint (Fig. 6H). Controlling WRTs to very slow runs thus, paradoxically, involves an increase in positive mechanical limb work, which is directed to accelerate the COM vertically.
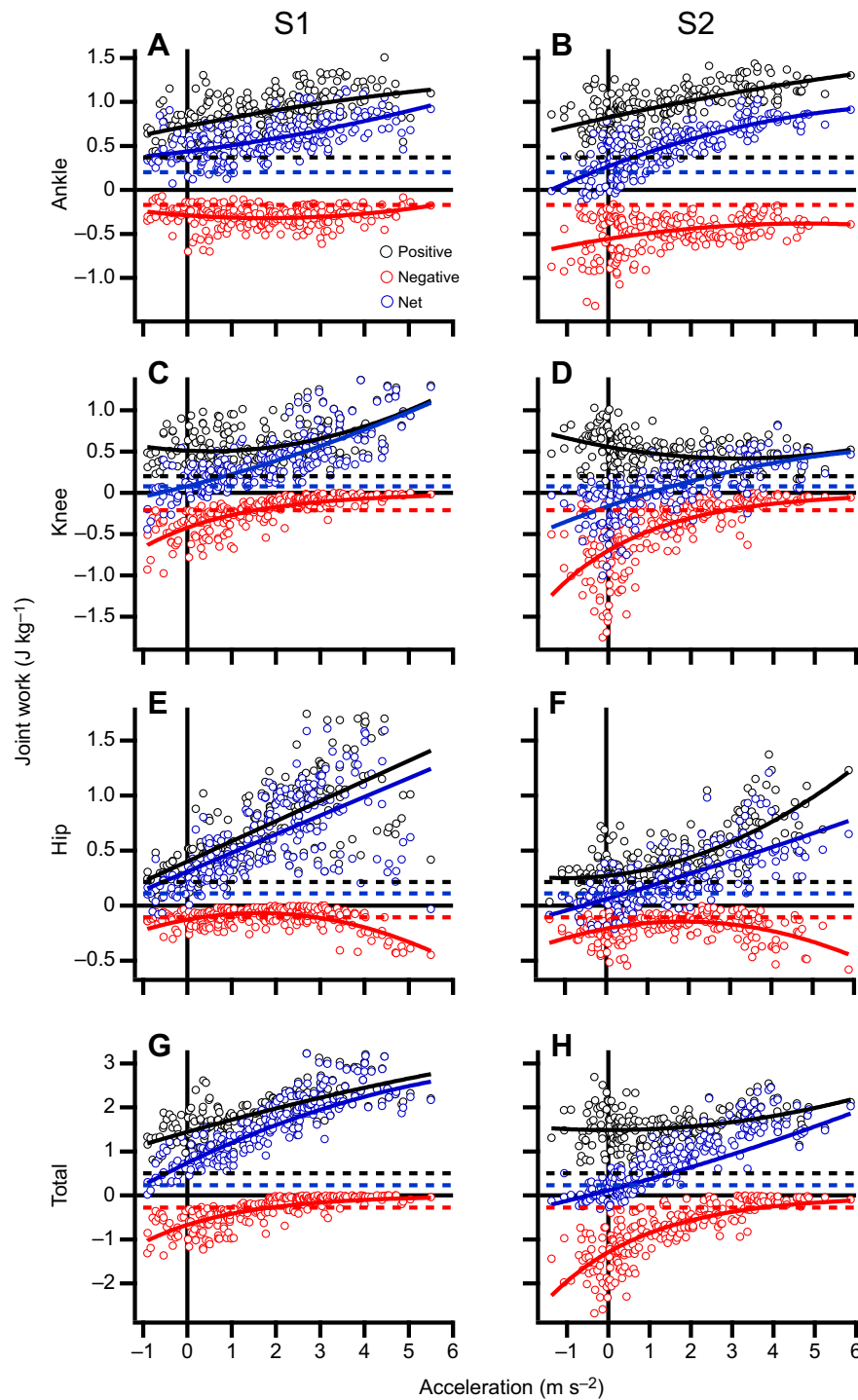
Fig. 6. Grouped positive, negative and net body-mass-specific mechanical joint work for each participant (*n*=10). Values for the ankle (A,B), knee (C,D) and hip (E,F) joints, and the total joint work (G,H), are shown for S1 and S2 plotted against the participants' average acceleration. Solid colored lines are lines of best fit. The dashed black, red and blue horizontal lines represent the amount of positive, negative and net mechanical work produced by each joint, respectively (A–F), or the positive, negative and net total joint work (G,H), when participants walked at their preferred velocity (v_{walk}).

By parsing total joint work into vertical and horizontal work, we uncover a previously undescribed (to the best of our knowledge) modulation of limb work in WRTs. With transitions to faster running, there is a clear systematic reduction in vertical limb work and an increase in horizontal limb work. When transitioning to a sprint, limb work is directed nearly exclusively in the horizontal direction compared with the near exclusive vertical limb work when transitioning to very slow runs (Fig. 5). This modulation can be viewed as an optimization for maximal forward acceleration when the goal is to achieve maximal running velocity, and minimization of forward acceleration when the goal is to achieve minimal forward velocity.

Limb mechanics of WRTs: insights into gait transition energetics and gait selection

Previous studies have found that gait transition is metabolically expensive (Usherwood and Bertram, 2003), especially when compared with the cost of changing speed by walking faster and slower (Minetti et al., 2013; Seethapathi and Srinivasan, 2015). Although we do not assess metabolic energy cost directly, our data corroborates these observations. We found that a WRT step that does not alter gait velocity is more costly of positive mechanical work compared with a normal walking step at the same velocity [positive work is used here as it is most closely associated with positive fiber
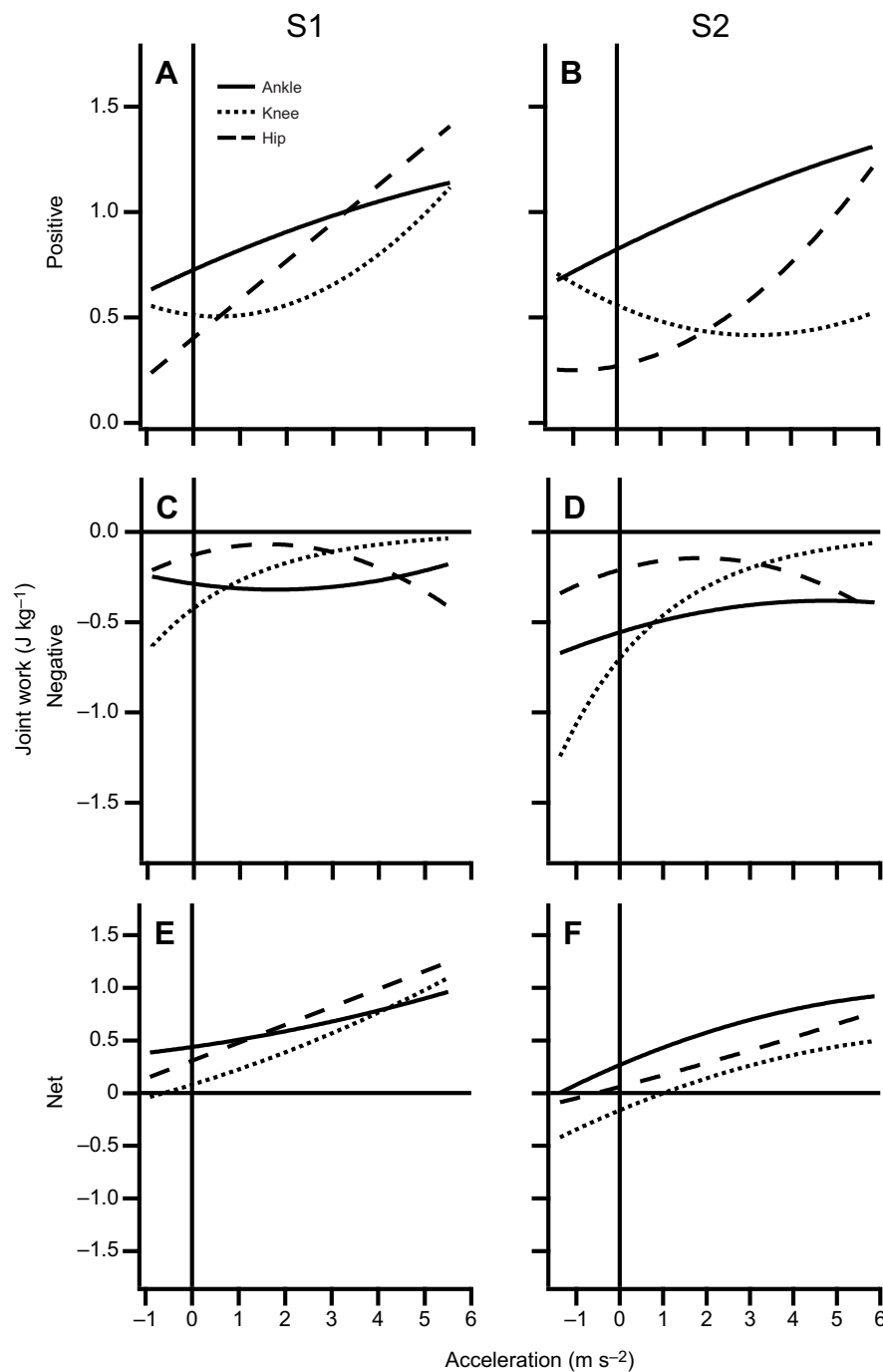
Fig. 7. The lines of best fit for positive, negative and net joint work versus acceleration for the ankle, knee and hip. The plots highlight the joint's contribution to the mechanical work of the step and how these contributions change with increasing acceleration.

work during gait (Sasaki et al., 2009) and metabolic energy (Woledge et al., 1985)]. We also found that changing velocity by walking faster/slower uses considerably less positive mechanical work than a gait transition to the same velocity (Fig. 9). These findings offer a possible mechanical underpinning to the relative costs of gait transitions and walking velocity oscillations, although comparisons to previous studies are complicated by the fact that these involved continuous walking/running in treadmill-bases experiments.

In addition to gait transition costs, our data provides insight into gait selection behavior. In an elegant study, Long and Srinivasan (2013) showed that human participants often use mixtures of walking and running gaits in an energetically optimal way to reach their destination. When the average velocity required for the journey decreased below ~2 m s^{-1}, however, participants used nearly exclusively a range of walking velocities. Our findings afford an explanation for this demarcation. First, transitions from walking to running are (unnecessarily) mechanically and metabolically expensive at these slow velocities and oscillating between walking slow and fast may instead be the most economical gait pattern. Furthermore, the very high mechanical cost of switching from walking to running at relatively slow velocities might diminish the benefit of walk–run mixtures utilizing slow, but metabolically economical, running velocities (2–2.5 m s^{-1}; Long and Srinivasan, 2013). These possible influences of WRT costs on gait behavior should in theory be amplified when distances are short and the relative cost of WRTs to the total cost of the journey are high.
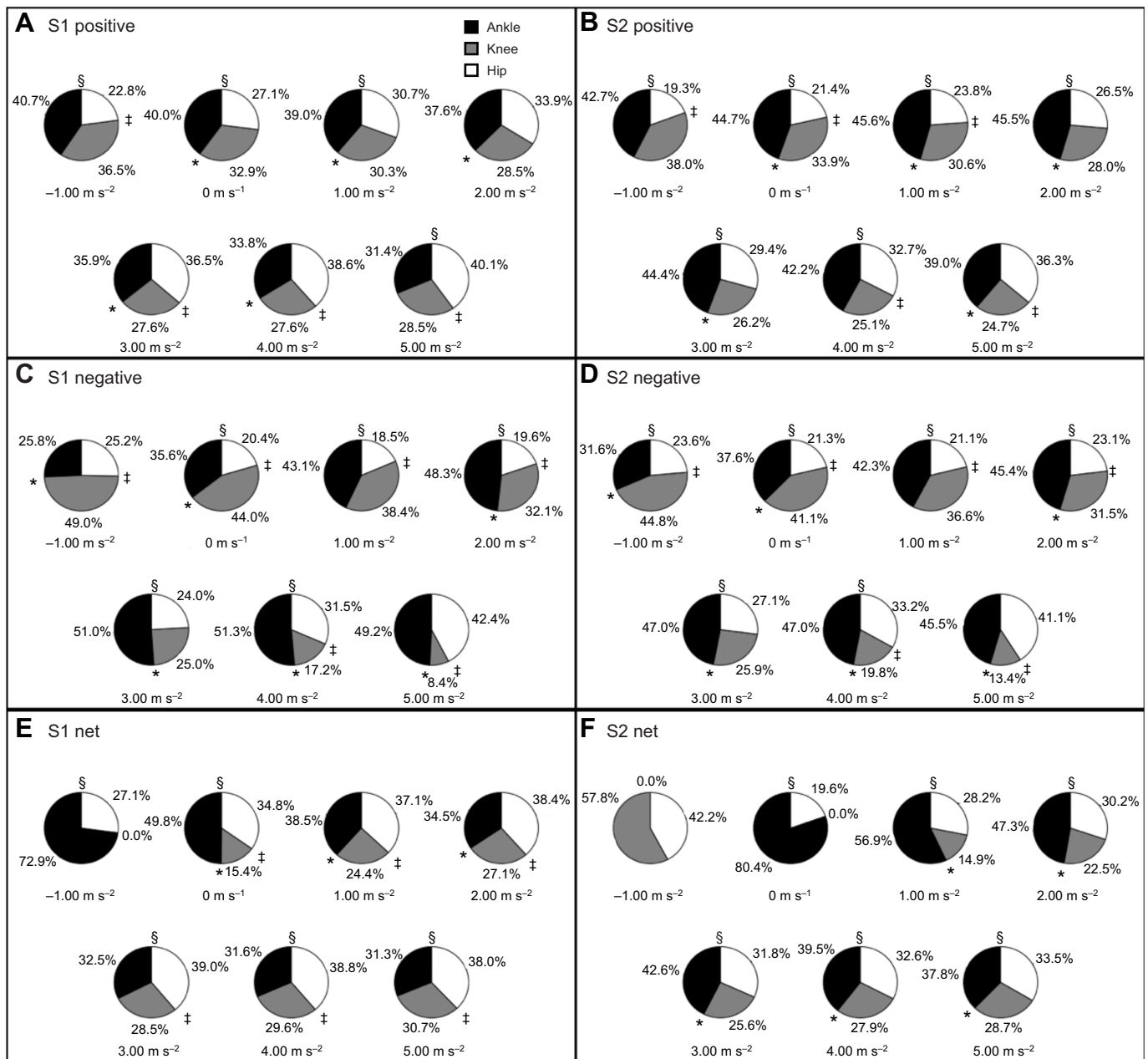
Fig. 8. The group average (*n*=10) percent joint work of the summed positive, negative and net joint work in S1 and S2. Ankle (black); knee (gray); hip (white). Percent contribution was computed at accelerations of −1.0, 0, 1.0, 2.0, 3.0, 4.0 and 5.0 m s^{-2}. To assess the contribution of each joint to net mechanical work, if the total net work was positive or negative, only the joints that were producing net positive or negative work, respectively, were included in the calculation of the percent joint work contribution. The symbols (*,‡,§) represent a significant difference between the ankle and knee, the knee and hip, and the ankle and hip, respectively (*P*<0.05).

Modulation of net joint work in walk-to-run transitions

We observed a more even distribution of net work across WRT accelerations than what was expected. Previous studies of incline running and jumping have found that the hip contributes substantially to the net mechanical work required to raise the COM (Roberts and Belliveau, 2005; Hubley and Wells, 1983). During incline running, it has been found that humans even decrease their net ankle work between moderate and steep inclines, relying purely on the hip to provide the additional COM mechanical work (Roberts and Belliveau, 2005). In contrast, we found that, overall, the ankle was at least equally important in providing net positive mechanical work as the hip in WRTs (ANOVA main effect). In fact,

in S2, the ankle bore the largest contribution to net work production even at the highest accelerations (Fig. 8F). Also noteworthy is the relatively large contribution of net positive mechanical work at the knee, especially in S1 (Figs 6C, 7E and 8E), which stands in contrast to the exclusive net negative knee work observed in human incline running. The obvious difference between the work distribution in incline running and jumping and the work distribution of the WRT is that work in WRTs is required to accelerate the COM forward, compared with vertical acceleration in the previous two tasks. This demonstrates that modulation of net joint work is not necessarily dictated by muscle–tendon architecture as much as it is by the mechanics of the locomotor task itself. Interestingly, the observed
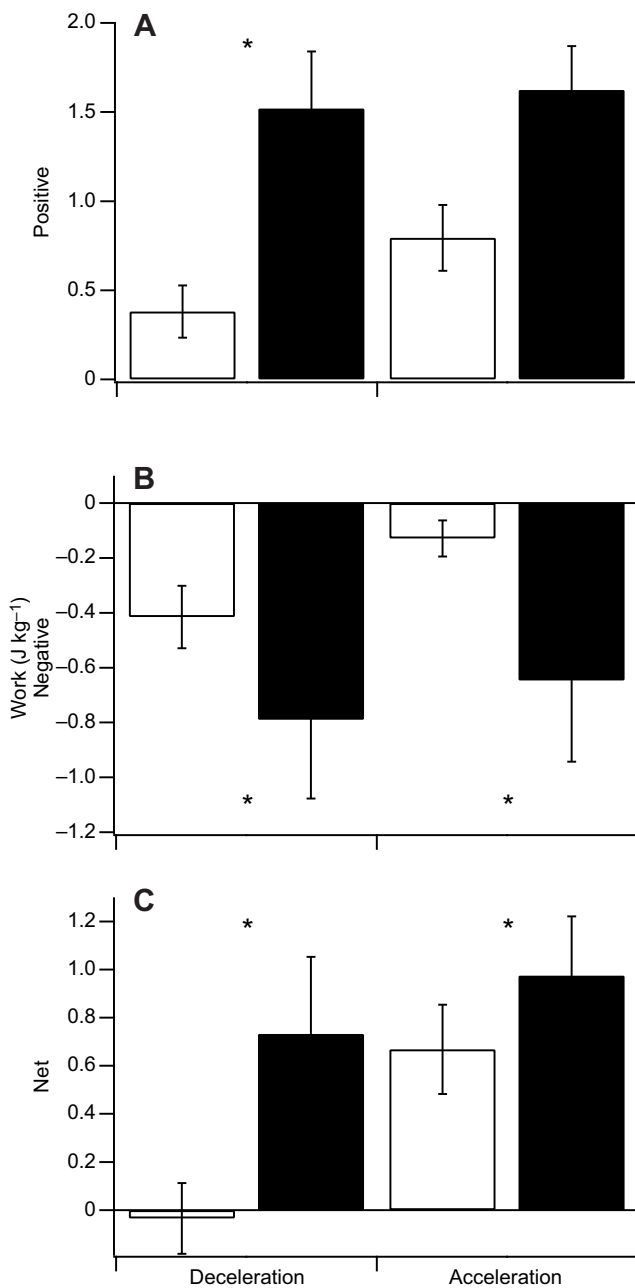
Fig. 9. Positive, negative and net total joint work. Work was measured as participants accelerated (0.49±0.32 m s^{-2}) or decelerated (−0.47±0.15 m s^{-2}) without changing gait (continuous walking; white bars) versus when transitioning to a run (WRT) with the same acceleration and deceleration [black bars; data are only presented for the first step of the WRT (S1)]. The asterisk (*) indicates a significant difference between the work generated in the walking acceleration/deceleration and that generated in the WRT acceleration/deceleration (P<0.05).

net work distribution between joints resembles those of other bipeds, turkeys and wallabies, undergoing a similar range of horizontal accelerations (Roberts and Scales, 2004; McGowan et al., 2005).

Notwithstanding the large contribution of the ankle to net work, our data does partially support our hypothesis that high acceleration WRTs are achieved by an increased reliance on net work at proximal joints, specifically the hip. This can be seen by the switch to predominantly hip-based net work production above 3 m s^{-2} in S1

(Fig. 8E). That this does not occur in S2, however, further illustrates that a distal-to-proximal modulation of net joint work depends on the locomotor context, not simply the magnitude of the required mechanical work. It is also noteworthy that the knee is responsible for the majority of the energy absorption (net negative work) during deceleration WRTs (Fig. 8F). This is consistent with the primary energy absorption role of the knee joint during constant-velocity walking and running (Novacheck, 1998; Hreljac et al., 2008; Farris and Sawicki, 2011b; Pires et al., 2014).

Modulation of positive joint work in walk-to-run transitions

During gait, absolute positive joint work is a much closer estimate of total positive muscle fiber work than net joint work (Sasaki et al., 2009) and, therefore, modulation of positive joint work (more so than net work) may be more closely linked with muscle–tendon architecture. Indeed, positive hip joint work in both S1 and S2 better align with our hypothesis that higher accelerations lead to a greater reliance on mechanical work production at proximal joints. These results also corroborate those of other studies investigating horizontal acceleration movements in humans showing an increased reliance on the hip for positive work (Belli et al., 2002; Farris and Raiteri, 2017).

A common explanation for a distal-to-proximal shift in work production has been that proximal joints are powered by strap-like muscles with long parallel fibers that are thought to be better suited to producing positive mechanical work compared with shorter, pennate, fibered muscles. Although the mass-specific work capacity of pennate muscles are not lower (any loss in shortening capacity due to short fibers can be offset by an increase in force capacity due to greater cross-sectional area), under high power demands, force–length–velocity effects may limit their force, and thus work capacity (Biewener and Roberts, 2000). An additional constraint on work capacity in distal muscles may be related to tendon compliance. Tendon compliance has the ability to affect muscle dynamics significantly, in particular as the time course for force production decreases (Lichtwark and Wilson, 2006; Lichtwark et al., 2007; Rosario et al., 2016). For example, it has been hypothesized that fast walking is avoided because the gastrocnemius and soleus must undergo rapid shortening that reduces force capacity due to fiber force–velocity effects (Neptune and Sasaki, 2005; Farris and Sawicki, 2011a). Similarly, using a simulation approach, Dorn et al. (2012) found that, when humans approach sprinting velocities, the triceps surae also shortens under high velocity and likewise has a compromised force capacity at these fast running velocities. It is possible that the interaction between the compliant Achilles tendon and the fiber mechanics of the triceps surae underscores the observed shift to greater reliance on the hip for positive work production during high-acceleration movements. Interestingly, greyhounds, which are characterized by highly compliant distal tendons, have similarly been shown to switch from positive joint work at the ankle to positive hip joint work as whole-body acceleration requirements increase (Williams et al., 2009).

We also demonstrate that, like net work, high positive mechanical work output is not limited to the hip joint. When transitioning to very slow running velocities, a surprisingly large amount of positive work is performed by the knee joint (Figs 6C,D and 7A,B). It is not clear why the knee, as opposed to the other joints, is used to produce the positive work in WRTs to slow running. One reason may be that the knee is better suited to produce vertical work compared with the hip. The predominant use of the knee extensors to power vertical jumping in humans provides support for this interpretation (Hubley

and Wells, 1983; Jacobs et al., 1996). We propose that the knee is preferentially recruited for positive vertical work, whereas the hip is recruited for positive horizontal work production in WRTs. This interpretation is borne from the combined modulation between positive knee and hip work and positive vertical and horizontal limb work across WRT accelerations. This is most apparent in S2, where the knee and hip exhibit a near opposite response to a change in WRT acceleration; here, the knee reduces positive work output at high accelerations that require predominantly horizontal work (Figs 6D, 7A). It is not clear whether this should result from any musculoskeletal architectural differences between knee and hip muscles, although it has been demonstrated, at least in cat locomotion, that certain muscles are more strongly related to controlling vertical versus horizontal GRFs (Kaya et al., 2006).

Limitations

This study focused solely on joint-level inverse dynamic analyses, and so represents the net effect of all muscles and structures of the joints. We have not taken into account co-contraction between antagonist muscles, force sharing between synergist muscles, energy transfer between joints, or the distribution of work and power between muscle fibers and tendons. The approach we have taken in this study may thus not reflect the mechanics of individual muscles. It also is possible that training may improve the effectiveness of unnaturally slow transition velocities, possibly altering their limb and joint mechanics.

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