

RESEARCH ARTICLE

The energetic function of the human foot and its muscles during accelerations and decelerations

Ross E. Smith, Glen A. Lichtwark and Luke A. Kelly*

ABSTRACT

The human foot is known to aid propulsion by storing and returning elastic energy during steady-state locomotion. While its function during other tasks is less clear, recent evidence suggests the foot and its intrinsic muscles can also generate or dissipate energy based on the energetic requirements of the center of mass during non-steady-state locomotion. In order to examine contributions of the foot and its muscles to non-steady-state locomotion, we compared the energetics of the foot and ankle joint while jumping and landing before and after the application of a tibial nerve block. Under normal conditions, energetic contributions of the foot rose as work demands increased, while the relative contributions of the foot to center of mass work remained constant with increasing work demands. Under the nerve block, foot contributions to both jumping and landing decreased. Additionally, ankle contributions were also decreased under the influence of the block for both tasks. Our results reinforce findings that foot and ankle function mirror the energetic requirements of the center of mass and provide novel evidence that foot contributions remain relatively constant under increasing energetic demands. Also, while the intrinsic muscles can modulate the energetic capacity of the foot, their removal accounted for only a 3% decrement in total center of mass work. Therefore, the small size of intrinsic muscles appears to limit their capacity to contribute to center of mass work. However, their role in contributing to ankle work capacity is likely important for the energetics of movement.

KEY WORDS: Foot energetics, Intrinsic foot muscles, Nerve block, Foot and ankle function, Jumping, Landing

INTRODUCTION

During steady-state locomotion, humans conserve mechanical energy at the center of mass (COM) by utilizing passive elastic tissues such as the Achilles tendon and plantar aponeurosis (Minetti et al., 1993; Soo and Donelan, 2012). These tissues can store and return mechanical energy, aiding in movement economy (Sawicki et al., 2009; Stearne et al., 2016). During non-steady-state locomotion, COM energetic demands exceed contributions from passive tissues alone and are met by dissipating or generating energy through muscle work about joints of the leg (Daley and Biewener, 2003; Devita et al., 2008). These conditions are present in everyday tasks such as walking initiation or turning, and

they involve frequent decelerations or accelerations (Orendurff et al., 2008). The majority of the literature examining COM work demands during decelerative and accelerative tasks focuses on work contributions from muscles acting about the ankle, knee and hip joints. The contributions of the foot have been comparatively neglected, despite a growing body of literature highlighting the potentially important energetic contribution of the foot to human locomotion (Kelly et al., 2015; Farris et al., 2019).


Historically, the foot is described as behaving like a passive spring during locomotion (Ker et al., 1987). During the stance phase of gait, the longitudinal arch lowers and lengthens (compresses), storing energy in the stretched plantar ligaments and plantar aponeurosis before rising and shortening (recoiling) just prior to take-off, releasing the stored energy to contribute to upward and forward acceleration of the COM (Ker et al., 1987). The foot also dissipates energy via the viscoelastic plantar fat pads of the heel and forefoot, which can dissipate between 20% and 50% of the energy they absorb (Bennet and Ker, 1990; Ledoux and Blevins, 2007). Considering the combined contribution of the plantar fat pads and plantar aponeurosis, it has recently been suggested that the foot is more akin to a spring-damper system during steady-state locomotion (Kelly et al., 2015; Takahashi et al., 2016).

In addition to the foot's passive contributions, the largest intrinsic foot muscles, the flexor digitorum brevis (FDB) and abductor hallucis (AH), have muscle-tendon units (MTUs) that actively lengthen and shorten during the stance phase of locomotion, qualifying them as a potential source of mechanical energy dissipation and generation (Kelly et al., 2015). The contribution of these muscles to the energetic function of the foot and ankle during constant-speed locomotion was recently revealed via the use of a selective nerve block to temporarily remove active force production within the foot. This produced a substantial drop in positive work performed at the foot (~30%) and also at the ankle (~10%) (Farris et al., 2019).

Beyond constant-speed locomotion, the potential for the intrinsic foot muscles to modulate the energetic behavior of the foot during accelerative and decelerative tasks has been recently reported (Riddick et al., 2019). Using simple stepping tasks to produce net-negative, net-zero and net-positive work demands at the COM, this study provided the first evidence that the foot could actively transition from a mechanical damper to a spring or motor, depending on whole-body energy requirements. The foot's overall contribution to COM energetics was reported to be 5–15% of net energy COM work (Riddick et al., 2019). However, the magnitudes of COM work and power reported for the stepping tasks were quite small, so it is unknown whether foot contributions remain constant during tasks with greater net-work requirements. Because of the relatively small physiological cross-sectional area of the intrinsic foot muscles, their force generating and, thereby, energetic contributions may be limited, especially as COM energy demands

School of Human Movement and Nutrition Sciences, The University of Queensland, Brisbane, QLD 4072, Australia.

*Author for correspondence (l.kelly3@uq.edu.au)

 R.E.S., 0000-0003-2776-8565; G.A.L., 0000-0001-7366-3348; L.A.K., 0000-0002-9736-0517

Received 21 January 2021; Accepted 13 May 2021

increase (Farris et al., 2019; Riddick et al., 2019). A recent study by Olsen et al. (2019) provides some insight that the foot can contribute to energy dissipation during rapid deceleration tasks. They reported ~11% of the total lower-body energy dissipation during drop landings from 0.4 m was performed about the mid-tarsal joint of the foot (Olsen et al., 2019). This suggests that the energetic contribution of the foot remains constant relative to the magnitude of COM work. However, the contribution of the intrinsic foot muscles to this energy dissipation remains unknown and needs to be clearly established.

The aim of this study was to quantify the energetic contributions of the foot and its intrinsic muscles during tasks requiring rapid energy dissipation and generation. To do this, we designed an experimental protocol where subjects performed sub-maximal jumps (accelerations) and drop landings (decelerations) over a range of prescribed heights. We hypothesized that the structures within the foot would dissipate more energy as drop landing height increased and generate more energy as jump height increased. However, because of the small size of the muscles, we further hypothesized that the relative contribution of the foot to COM work would plateau during the tasks that required the greatest deceleration or acceleration of the COM. In order to isolate intrinsic foot muscle contributions, a tibial nerve block was applied to temporarily prevent activation of the muscles. Subjects then completed an identical protocol, allowing a comparison between task performance with and without foot muscles actively producing force and performing work. Given the previously described functional coupling between the foot and ankle (Kelly et al., 2015; Farris et al., 2019; Riddick et al., 2019), we hypothesized that foot and ankle work magnitudes for decelerative and accelerative tasks would decrease in the blocked (BL) condition compared with the non-blocked (NB) condition.

MATERIALS AND METHODS

Participants

We recruited 15 recreationally active individuals (11 males, 4 females, 28.4±10.9 years old, 1.75±0.20 m, 74.5±16.13 kg, means±s.d.) who were between 18 and 45 years old, were able to walk and run comfortably for 30 min, and had no serious lower limb injury in the previous 12 months. Because of issues with marker reconstruction, the data from two subjects were excluded from the jumping conditions. Additionally, we were unable to obtain an adequate nerve block in two subjects; therefore, their data were also excluded from the analysis (landing data $n=13$; jumping data $n=11$). This study was approved by The University of Queensland's Human Research Ethics Committee and conducted in accordance with the Declaration of Helsinki. All participants provided written informed consent to participate.

Experimental task

Participants performed a series of single-leg drop landings from three heights (H1=20.5 cm, H2=30.5 cm, H3=40.5 cm). They also performed a series of single leg sub-maximal jumps to three prescribed heights (H1=10.5 cm, H2=15.5 cm, H3=20.5 cm). The drop landings and sub-maximal jumps were completed in a randomized order to remove any order effects. Prior to the collection of experimental data, participants underwent a familiarization procedure to learn how to successfully complete each task and ensure that they were comfortable with the experimental environment. The complete protocol (landings and jumps, outlined below) was performed twice, once before and once after a selective nerve block was administered in order to temporarily remove the force-producing capabilities of the intrinsic foot muscles.

For the drop landings, participants were cued to step out horizontally from the box with their lead leg, allowing the COM to progress beyond the stance foot to initiate falling. Lead leg determinacy was established by asking the participant which leg they would use if striking a soccer ball. A landing trial was deemed successful when the participant stepped down from the box onto the lead foot/leg and the COM velocity returned to zero without ground contact from the contralateral foot. For the sub-maximal jumps, participants were asked to initiate balance on their lead leg, then jump from that leg to a box that was located slightly in front of them. A trial was deemed successful if the participant assumed a unilateral stance on the lead foot/leg, then initiated a countermovement and subsequent jump onto the respective box height without any ground contact from the contralateral foot. The nature of the unilateral task imposed a balance constraint on task completion, so the use of arms for balance and arm swing was permitted.

Peripheral nerve blocks

A nerve block was applied to the distal aspect of the tibial nerve of the lead leg, 2–4 cm proximal to the medial malleoli, under ultrasound guidance. This procedure was undertaken to temporarily remove activation of the intrinsic foot muscles without directly influencing the activation of the extrinsic foot muscles or ankle plantar flexors. The anesthetic dosage (2% lignocaine plain solution) never exceeded more than 3 mg kg⁻¹, in accordance with local state law. Because of this restriction, the nerve block was only applied to the lead leg in order to ensure a full motor block in one foot. For safety reasons, the fine wire EMG electrodes were removed from the intrinsic foot muscles prior to the application of the nerve block. To determine the efficacy of the block, skin-mounted surface EMG electrodes were placed over the arch of the foot to record generalized muscle activation patterns immediately prior to, and following, the administration of the block. We ensured active toe flexion (without toe curling) was appreciably diminished, then further confirmed the motor block through the absence of a surface EMG signal along the medial arch of the foot.

Data collection and analysis

Motion capture and ground reaction force data

Retro-reflective markers (6.4 mm, B&L Engineering, Santa Ana, CA, USA) were placed on the lead foot just below the Achilles tendon insertion in order to define a calcaneus segment (Leardini et al., 2007; Kelly et al., 2014). Additionally, individual reflective markers were secured using double-sided adhesive tape on both lateral and medial malleoli, lateral and medial epicondyles, and on the left and right anterior and superior spines of the iliac crest to model the shank, thigh and pelvis segments (Leardini et al., 2007). Rigid plates with four markers were placed on the lateral aspect of the shank and thigh and secured with neoprene wraps for tracking segments during motion. A static calibration trial was taken to establish joint centers and segment coordinate systems and dimensions. Then, malleoli and epicondyle markers were removed and the remaining markers were used during experimental trials to track motion of the lower limb and foot. Marker trajectories were recorded with an 11-camera three-dimensional (3D) motion capture system (Oqus, Qualisys AB, Göteborg, Sweden).

Ground reaction force (GRF) data were collected synchronously with motion capture data from a force plate mounted flush with the laboratory floor (AMTI, OR6-7-1000, Watertown, MA, USA). The GRF data were collected from the lead leg during the ground contact phase of each experimental task between 1250 and 5000 Hz, and were subsequently analog-to-digital converted

using the previously described motion capture system. Marker trajectory and GRF data were exported to Visual 3D (Visual3D, C-Motion, Inc., Germantown, MD, USA). For drop landings and jumps, GRF and motion data were low-pass filtered at 25 Hz. The frequencies were matched so as to avoid the possibility of creating moment artefacts in the sagittal plane (Derrick et al., 2020). All GRF data were then down-sampled to match the frame rate of kinematic data.

For drop landings, all kinetic variables that are reported occurred during the time from ground contact until the approximate cessation of the landing, when velocity of the body went to zero. This period is defined as the frame when the vertical component of the GRF signal exceeded 50 N (foot contact) until the frame where pelvis-segment velocity was no longer negative (landing completion).

Kinetic data for jump variables were calculated from countermovement initiation, defined as the frame where pelvis-segment velocity descended under a -0.075 m s^{-1} threshold, to the take-off, where the vertical component of GRF reached zero. Optimally, we would have preferred to use any descent into negative velocity as the countermovement initiation cut-off threshold; however, the unilateral nature of the task imposed a balance constraint where pelvis-segment velocity would frequently oscillate just above and under zero before initiating a jump, rendering our preferred method inadequate.

For our model of foot energetics, we used a unified deformable (UD) segment analysis to measure the foot's contributions to COM energetics. The formula and rationale for this analysis are described in previous literature (Takahashi et al., 2012, 2017). This method treats the foot as a deformable segment with a rigid proximal component (calcaneus) and an anteriorly located deformable component, which allows estimation of mechanical power generated by the interaction of the foot with the ground (Kelly et al., 2015; Takahashi et al., 2016). The cumulative integral of foot power (work) indicates the mechanical work performed by all structures within the foot, distal to the calcaneus.

We used an inverse kinematic model to calculate joint kinematics, with an inverse kinematic chain from pelvis to thigh, thigh to shank, and shank to calcaneus, where rotations about the sagittal, frontal and transverse planes were permitted, while translational components were only allowed at the hip. In accordance with recommendations from Lu and O'Connor (1999), the ankle joint's constraint was weighted doubly in the global optimization from the other joints in order to correct for soft tissue and movement artefact. Joint rotations were expressed within their proximal segments' coordinate systems and were defined as follows: hip as thigh about pelvis; knee as shank about thigh; ankle as calcaneus about shank. Force polarity was positive for the proximal, lateral and anterior directions, and joint moment polarity was determined by the right-hand rule of the segment's coordinate system where X was the longitudinal axis, Y was the anteroposterior axis, and Z was the mediolateral axis. Net internal joint moments (N m) were calculated using a Newton-Euler inverse dynamic approach. Segment mass, moment of inertia, joint center location and COM location used for all inverse dynamic calculations were Visual 3D definitions (Dempster, 1955; Hanavan, 1964). Joint power was computed as the dot product of moment and respective joint velocity. Joint work was computed by trapezoidal integration of respective joint power. All joint moment, power and work values were normalized to body mass and reported for the sagittal plane, other than the UD foot segment, which was a 6-degree of freedom calculation.

The COM power for all tasks was calculated as the dot product of the vertical component of ground reaction force (GRF_V) and COM velocity, and is summarized by the following equation:

$$\text{COM power} = \text{GRF}_V \cdot \int ((\text{GRF}_V - \text{body weight})/M) dt, \quad (1)$$

where the second term represents COM velocity, calculated by trapezoidal integration of COM acceleration, or GRF_V minus the product of body mass and gravity (body weight), divided by body mass (M) with respect to time (dt). COM work was calculated by trapezoidal integration of COM power. For drop landings, an initial COM velocity integration constant was estimated using the pelvis segment velocity just before foot contact. All power and work metrics were normalized to body mass (W kg^{-1} and J kg^{-1} , respectively).

Muscle activation

Fine wire electromyography (EMG) electrodes (0.051 mm stainless steel, Teflon coated, Chalgren, Gilroy, CA, USA) were inserted into the AH and FDB muscles under ultrasound guidance (10 MHz linear array, SonixTouch, Ultrasonix, Richmond, BC, Canada) in accordance with previously described techniques (Kelly et al., 2014, 2015, 2018) and connected to discrete pre-amps. Two pairs of surface EMG electrodes with inter-electrode center distances of 20 mm (Tyco Healthcare Group, Neustadt, Germany) were adhered to the skin overlying the muscle tissue of the tibialis anterior (TA) and medial gastrocnemius (MG). The EMG data were collected at 4000 Hz and amplified 1000 times using band-pass filtering of 30–1000 Hz for fine wire data and 30–500 Hz for surface EMG data (MA-416, Motion Lab Systems, Baton Rouge, LA, USA). The skin where the surface electrodes were to be placed was shaved, abraded and cleaned with isopropyl alcohol wipes prior to electrode mounting. All EMG signals were processed using a custom-written script in Matlab (MathWorks, Natick, MD, USA) to remove DC offsets, filter data using a second-order Butterworth high-pass filter (35 Hz for surface, 50 Hz for intrinsic), rectify the signal, then filter the rectified signal with a 10 Hz low-pass filter to smooth the data.

For drop landings, mean signal amplitude was calculated for all muscles from ground contact to landing completion (as described above). Additionally, a 0.32 s time window was used to capture muscle activity during the descent of landing in order to detect pre-activation before ground contact. For jumps, mean rectified signal amplitude was calculated for all muscles during the period from countermovement initiation to take-off (as described above).

Statistics

A priori analysis (G*Power, Düsseldorf, Germany) revealed a 12 participant pool with an estimated moderate effect at $d=0.5$, power of $\beta=0.9$ and an alpha level of $P=0.05$ for the effect of the block on foot contributions to both tasks. Two-way, within-subjects, repeated measures analyses of variance (SPSS 23.0, Chicago, IL, USA) were performed to determine the effect of manipulating COM net positive (jumping) and net negative (landing) mechanical work (height) and removing active force production from intrinsic foot muscles (condition) on UD foot and ankle kinetics and kinematics, as well as muscle activation data during landing and sub-maximal jumping tasks. If interaction effects were present, *post hoc* multiple comparisons were performed in order to detect the nature of the interaction. Bonferroni corrections were made to reduce the likelihood of type 1 error with multiple comparisons. Statistical significance was set at $P \leq 0.05$. Effect sizes reported are partial

Table 1. Group mean negative work for joints and center of mass (COM) during landing

Landing	Blocked			Non-blocked			Condition		Height	
	H1	H2	H3	H1	H2	H3	<i>P</i>	η_p^2	<i>P</i>	η_p^2
Work (J kg ⁻¹)										
Foot	-0.29±0.11	-0.35±0.12	-0.44±0.17	-0.36±0.11	-0.46±0.20	-0.60±0.19	0.015**	0.403	0.001*	0.738
Ankle	-0.82±0.36	-1.03±0.29	-1.18±0.26	-0.98±0.20	-1.16±0.28	-1.45±0.33	0.003**	0.534	<0.001*	0.864
COM	-2.28±0.88	-3.17±0.92	-3.93±0.94	-2.26±0.68	-3.16±0.74	-3.86±0.67	0.791	0.006	<0.001*	0.938
Work as % COM										
Foot	13.54±5.87	11.62±4.53	11.31±3.64	16.77±6.71	15.23±8.00	15.62±4.40	0.020*	0.377	0.288	0.202
Ankle	36.15±9.52	33.69±9.02	30.54±5.75	46.77±15.1	37.77±9.73	38.31±9.00	0.002*	0.560	0.017*	0.525

H1–3, height (20.5, 30.5 and 40.5 cm, respectively). Effect sizes are shown as partial eta squared (η_p^2) values. Statistical significance was set at $P \leq 0.05$.

*Significant main effect of height (COM work); **significant main effect of condition (nerve block).

eta squared (η_p^2) values where $\eta_p^2 < 0.2$ is trivial, $\eta_p^2 = 0.2–0.3$ is small, $\eta_p^2 = 0.3–0.7$ is moderate and $\eta_p^2 > 0.7$ is large. All results are reported as means±s.d.

RESULTS

Energy dissipation

Ankle kinematics

To provide insight into alterations in landing strategy due to drop landing height or the presence of a peripheral nerve block, we compared ankle angle at foot contact across all conditions. The ankle landed in greater plantar flexion as drop landing height increased (H1: -2.34 ± 6.65 deg, H2: -2.44 ± 6.98 deg, H3: -4.32 ± 6.75 deg, where plantar flexion is negative, $P = 0.004$). There was no change in ankle orientation at foot–ground contact observed in the presence of a nerve block, compared with the NB condition (BL: -3.78 ± 6.34 deg, NB: -2.28 ± 7.25 deg, $P = 0.151$).

COM and joint energetics

COM work increased with increasing landing height (see Table 1 for mean values; $P \leq 0.001$) and was not different between the BL and NB conditions ($P = 0.791$). Fig. 1A,B displays the rate of energy dissipation (negative power) at the foot and ankle during drop landings. There was a clear similarity in the general power patterns for the foot and ankle during the drop landing tasks. Energy dissipation (negative work) at the foot and ankle is presented in Fig. 1C,D, with descriptive statistics presented in Table 1. We observed a main effect of landing height for both the foot and ankle, with the magnitude of negative work increasing with drop height (foot: $P = 0.015$, ankle: $P = 0.003$). We also observed a main effect of the nerve block, with a significant reduction in the amount of energy dissipated at the foot and ankle in the BL condition (foot: $P = 0.001$, ankle: $P \leq 0.001$).

Fig. 1E,F shows the percentage contribution of the foot and ankle to COM work across all landing heights in the NB and BL conditions. As landing height increased, the foot's relative contribution to COM work remained unchanged ($P = 0.288$).

However, the contribution of the ankle to COM work declined as drop-landing height increased ($P = 0.017$). There was also a main effect of the nerve block for the relative contribution of the foot ($P = 0.020$) and ankle ($P = 0.002$) to COM work, with substantially less energy being dissipated about these joints in the presence of a nerve block. Landing duration between NB and BL conditions was not different ($P = 0.791$), which we report to ensure comparability of NB and BL conditions.

Muscle activation

Mean EMG values for AH, FDB, MG and TA and time series data for drop landings can be found in Table 3 and in Fig. S1, respectively. No main effects between BL and NB conditions were observed for either the MG or TA ($P = 0.174$, $P = 0.176$, respectively). However, main effects for height were observed for all muscles, where activity increased as height increased (AH $P = 0.015$, FDB $P = 0.019$, MG $P = 0.005$, TA $P = 0.033$).

Energy generation

COM and joint energetics

Positive COM work increased as jump height increased (see Table 2 for mean values; $P \leq 0.001$) and did not differ between NB and BL conditions ($P = 0.682$). Fig. 2A,B displays the rate of energy generation (positive power) for the foot and ankle during the sub-maximal jumping tasks. Despite differences in magnitude, there was a marked similarity in the shape of ankle and foot power waveforms during jumping. Energy generation (positive work) at the foot and ankle during the jumping tasks is presented in Fig. 2C,D, with descriptive statistics reported in Table 2. The magnitude of energy produced (positive work) about the foot and ankle increased with increasing jump height (foot: $P = 0.004$, ankle: $P = 0.002$). There was also a significant effect of nerve block on work at the foot and ankle, with substantial reductions in positive work observed when participants jumped with a nerve block (foot: $P = 0.001$, ankle: $P = 0.005$).

Table 2. Group mean positive work for joints and COM during jumping

Jumping	Blocked			Non-blocked			Condition		Height	
	H1	H2	H3	H1	H2	H3	<i>P</i>	η_p^2	<i>P</i>	η_p^2
Work (J kg ⁻¹)										
Foot	0.28±0.10	0.31±0.11	0.34±0.11	0.37±0.10	0.40±0.11	0.42±0.11	0.001**	0.689	0.004*	0.710
Ankle	0.89±0.25	1.00±0.25	1.11±0.30	1.08±0.28	1.15±0.28	1.20±0.26	0.005**	0.567	0.002*	0.755
COM	2.95±1.17	3.44±1.34	3.74±0.90	3.00±1.07	3.40±1.13	3.96±1.44	0.682	0.017	<0.001*	0.873
Work as % COM										
Foot	10.45±4.60	9.45±3.31	9.18±2.56	13.36±5.33	12.36±4.13	11.27±3.80	0.001**	0.696	0.102	0.398
Ankle	32.27±9.80	30.91±8.78	29.82±6.27	38.64±12.2	35.45±8.25	32.73±9.50	0.010**	0.504	0.032*	0.536

H1–3, height (10.5, 15.5 and 20.5 cm, respectively). Effect sizes are shown as partial eta squared (η_p^2) values. Statistical significance was set at $P \leq 0.05$.

*Significant main effect of height (COM work); **significant main effect of condition (nerve block).

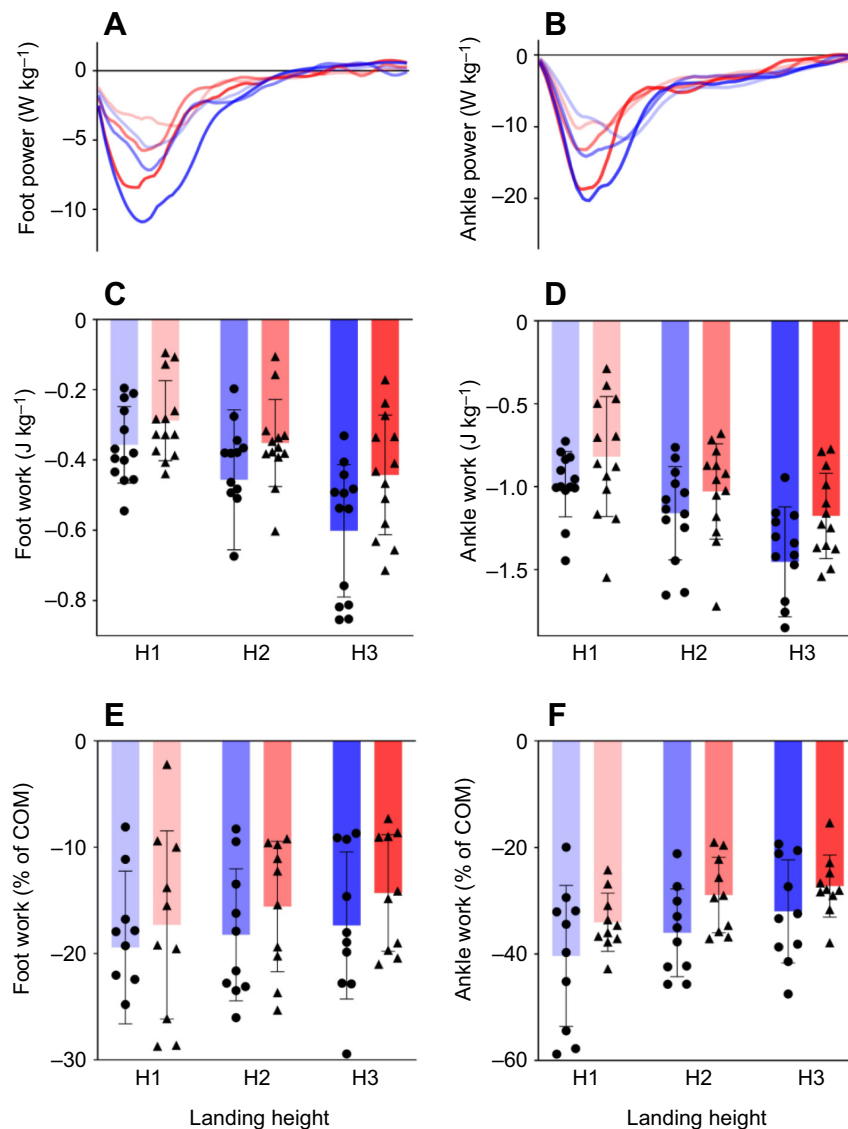


Fig. 1. Foot and ankle power and work during landing. (A,B) Group mean time series (normalized to 101 points) power curves for foot (A) and ankle work (B) during landing ($n=13$). The non-blocked (NB) condition is represented by blue lines, and the blocked (BL) condition by red lines. Heights (H1=20.5 cm, H2=30.5 cm, H3=40.5 cm) follow a transparency gradient where the lowest height is represented by the most transparent line and the highest is the most solid line. (C,D) Group mean negative work for the foot (C) and ankle (D) during landing. (E,F) The same values as a percentage of center of mass (COM) work multiplied by -1 for visualization purposes. Individual data points and means \pm s.d. are shown.

Fig. 2E,F shows the relative contribution of the foot and ankle to COM work across all three jump heights in both the NB and BL conditions. The relative contribution to positive work at the COM during the jumping tasks remained constant at the foot across all jump heights ($P=0.102$), while the relative contribution of the ankle to COM work decreased with increasing jump height ($P=0.032$). The relative contribution to COM work decreased in the BL condition compared with the NB condition for both the foot ($P=0.001$) and ankle ($P=0.01$). Task performance was not different between the NB and BL conditions, as COM work was similar at each sub-maximal jump height ($P=0.682$).

Muscle activation

Mean EMG values for the AH, FDB, MG and TA and time series data from the beginning of the countermovement until take-off during jumping can be found in Table 3 and Fig. S2, respectively. During jumping, no condition effects were observed for either the MG or TA muscles ($P=0.295$, $P=0.089$, respectively). Foot muscle activation showed no increases with increasing jump height (AH $P=0.170$, FDB $P=0.243$), but we did observe main effects for height for the MG and TA, where activity increased with increasing jump height (Table 3; MG $P=0.008$, TA $P=0.002$).

DISCUSSION

In this study, we sought to quantify the energetic contributions from the foot and its intrinsic muscles to tasks requiring large amounts of energy generation and dissipation at the COM. We hypothesized the magnitude of energy dissipated or generated at the foot would be modulated to match the COM work requirements. However, because of the relatively small sizes of muscles acting within the foot, we anticipated a plateau in the maximal work capacity of the foot at our highest work conditions. Our results indicate the foot's contributions to energy dissipation and generation remain relatively constant with increasing COM work demands. We observed a consistent reduction in work at the foot and ankle when the intrinsic foot muscles were unable to actively contribute to energy dissipation and generation. These data demonstrate that the energetic function of the foot can be adapted to meet the energetic demands of the whole body during tasks that require large accelerations and decelerations. The intrinsic foot muscles appear to make a substantial contribution to the adaptive function of the foot and ankle.

In agreement with our hypothesis, we found the magnitude of energy dissipated at the foot increased with increasing COM negative work demands. The increase in energy dissipation at the foot

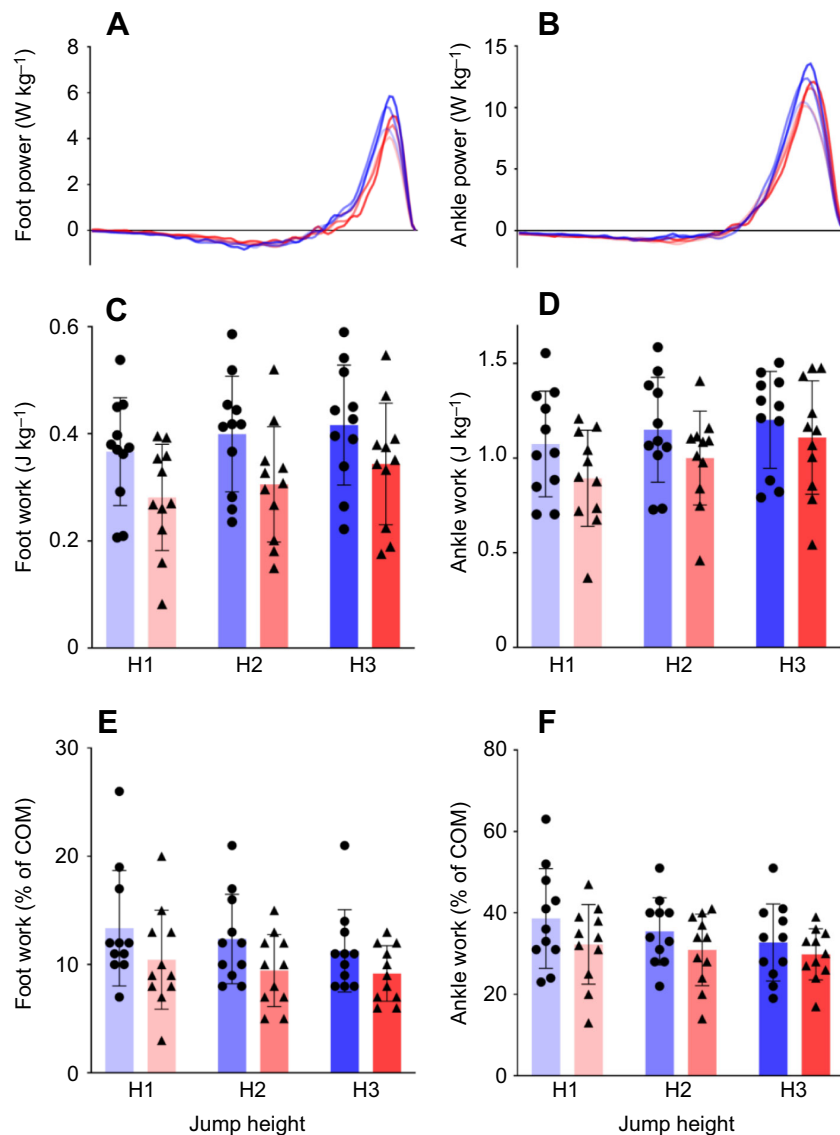


Fig. 2. Foot and ankle power and work during jumping. (A,B) Group mean time series (normalized to 101 points) power curves for foot (A) and ankle work (B) during jumping ($n=11$). The NB condition is represented by blue lines, and the BL condition by red lines. Heights (H1=10.5 cm, H2=15.5 cm, H3=20.5 cm) follow a transparency gradient where the lowest height is represented by the most transparent line and the highest is the most solid line. (C,D) Group mean positive work for the foot (C) and ankle (D) during jumping. (E,F) The same values as a percentage of COM work. Individual data points and means \pm s.d. are shown.

facilitated a constant, relative contribution to overall COM work demands across all landing heights. Contrary to our second hypothesis, we observed no plateau in negative foot work contributions as the energy dissipation requirements increased. Our results are similar to those of Olsen et al. (2019), who reported mid-

foot energy dissipation during drop landings (0.4 m) and found that between 8% and 11% of the COM work during landing was performed about the mid-foot (Olsen et al., 2019). Our data suggest that ~18% of the total COM negative work is performed at the foot during deceleration tasks. This finding is higher than Olsen et al.'s

Table 3. Group mean muscle activity for both landing and jumping

Muscle activity	Blocked			Non-blocked			Condition		Height	
	H1	H2	H3	H1	H2	H3	<i>P</i>	η_p^2	<i>P</i>	η_p^2
Landing (mV)										
AH	–	–	–	0.13 \pm 0.11	0.11 \pm 0.06	0.18 \pm 0.13	–	–	0.005*	0.355
FDB	–	–	–	0.07 \pm 0.04	0.09 \pm 0.10	0.08 \pm 0.04	–	–	0.610	0.040
MG	0.13 \pm 0.11	0.15 \pm 0.09	0.17 \pm 0.12	0.18 \pm 0.13	0.20 \pm 0.13	0.22 \pm 0.14	0.06	0.254	0.002*	0.406
TA	0.13 \pm 0.06	0.15 \pm 0.07	0.16 \pm 0.07	0.10 \pm 0.06	0.12 \pm 0.08	0.15 \pm 0.09	0.105	0.204	0.002*	0.418
Jumping (mV)										
AH	–	–	–	0.10 \pm 0.06	0.11 \pm 0.07	0.12 \pm 0.08	–	–	0.071	0.232
FDB	–	–	–	0.10 \pm 0.06	0.12 \pm 0.06	0.12 \pm 0.06	–	–	0.232	0.136
MG	0.21 \pm 0.10	0.23 \pm 0.10	0.24 \pm 0.11	0.24 \pm 0.07	0.26 \pm 0.07	0.28 \pm 0.07	0.316	0.100	<0.001*	0.505
TA	0.17 \pm 0.03	0.20 \pm 0.08	0.25 \pm 0.08	0.17 \pm 0.04	0.18 \pm 0.04	0.20 \pm 0.03	0.148	0.197	<0.001*	0.600

H1–3, height (20, 30 and 40 cm, respectively, for landing; 10.5, 15.5 and 20.5 cm, respectively, for jumping). AH, abductor hallucis; FDB, flexor digitorum brevis; MG, medial gastrocnemius; TA, tibialis anterior. Effect sizes are shown as partial eta squared (η_p^2) values. Statistical significance was set at $P \leq 0.05$. *Significant main effect of height (COM work); **significant main effect of condition (nerve block).

(2019) reported value, but similar to previous work (Riddick et al., 2019). The difference between our results and those of Olsen et al. (2019) are likely explained by differences in modelling of the foot and its joints. Olsen et al. (2019) reported only sagittal plane mechanical work performed about a mid-foot joint, whereas we used a UD model, which includes the dissipative contributions for all deformable tissues within the foot with 6 degrees of freedom. Our results further support the idea that the foot is well suited as a mechanical damper, playing a substantial role in absorbing energy during deceleration tasks, even when the requirements for energy absorption are high.

Ankle energy dissipation also increased with increasing COM work demands, yet the ankle's relative contributions to COM work decreased (41% to 34%) with increasing height. During bilateral landings, this same trend was observed by Zhang et al. (2000), who found net negative ankle work increased slightly, but the increase in net COM work primarily came from knee and hip contributions. The Achilles tendon appears to play an import role in absorbing energy during rapid decelerations, preventing excessively high muscle strain in the ankle plantar flexor muscles (Werkhausen et al., 2017). It is likely that the rate of energy absorption needed to decelerate the COM during our landing tasks exceeds that which can be effectively or safely buffered by the Achilles tendon. Therefore, landing would require proximal hip and knee muscular contributions, which are better suited for rapidly absorbing and dissipating large amounts of energy (Biewener and Roberts, 2000). We also suspect that a proportion of the additional energy dissipation at the COM with increasing height may have been performed by muscles acting about the frontal plane of the hip and ankle, in line with previous findings for single leg landings (Yeow et al., 2011).

During the accelerative jumping tasks, the magnitude of positive work performed (energy generation) at the foot increased with increasing jump height, while its relative contributions to COM work were unchanged. Contrary to our hypothesis, we did not observe a plateau in the contribution from the foot to COM work with increasing jump height. We have previously suggested that the energetic capacity of the foot may be limited as a result of the relatively small size and physiological cross-sectional area of the intrinsic foot muscles (Riddick et al., 2019; Farris et al., 2019). However, these data indicate that the foot can maintain a contribution of ~8% of positive work on the COM. This work must come from active contributions of the intrinsic and extrinsic foot muscles, or else be transferred from more proximal muscles.

In accordance with our hypothesis, the magnitude of positive work performed by the ankle increased as COM work demands increased. However, this occurred without a significant change in the ankle's relative contributions to COM work, despite the necessity for additional energy generation at the COM with increasing jump height. Results from Wade et al. (2018) indicate the ankle's contributions to COM energetic demands when maximally jumping are limited by the relative compliance of the Achilles tendon. Under the time constraints of jumping, proximal joint contributions tend to dominate positive work performed as jump height increases via transmitting force through relatively stiffer tendons. Previous authors have also found that as sub-maximal jump heights increased, the ankle's relative contributions remained constant while proximal joint contributions accounted for increases in jump height (Vanrenterghem et al., 2004, 2008). Our findings followed this trend, showing decreases in sagittal ankle work (3.5%) contributions with increasing jump height while sagittal knee and hip positive work contributions increased (1% and 3%, respectively) (see Fig. S5).

Upon removal of active contributions from the intrinsic foot muscles through a nerve block, we observed reductions in foot energy dissipation during landing and energy generation during jumping. Riddick et al. (2019) previously suggested the foot's damping and motor capacities are modulated by the intrinsic foot muscles. However, they were unable to parse the contributions from the intrinsic and extrinsic foot muscles, as well as the plantar aponeurosis. By implementing an experimental nerve block, we were able to directly quantify the contributions of the intrinsic foot muscles to energy dissipation and generation within the foot. During the deceleration tasks, our results showed a 19% reduction in negative work performed by the foot in the nerve block condition. This equates to a 3% reduction in the foot's contribution to COM work (see Table 1). Of note, even without the intrinsic foot muscles, the foot was still capable of dissipating 11–13% of net COM energy. This finding highlights the dissipative contributions of the foot's extrinsic foot muscles, which also dissipate energy during walking (Maharaj et al., 2017), as well as passive energy dissipation from the foot's fat pads and soft tissues. During the acceleration tasks, the foot's positive work output decreased by 22% in the nerve block condition, which also equates to a 3% reduction in relative COM work (see Table 2). The magnitude of foot muscle contributions to COM work is consistent with previous literature using a similar nerve block technique during constant speed locomotion (Farris et al., 2019). Our findings again reinforce the idea that the maximal work capacity of the intrinsic foot muscles at the COM may be limited by their small cross-sectional area (Farris et al., 2019; Riddick et al., 2019). The substantial proportion of mechanical energy generated by structures acting at the foot in the absence of intrinsic foot muscle activation (~9%) highlights the potentially important role of the extrinsic foot muscles, or energy transfer from more proximal muscles.

The temporary removal of active force production from the intrinsic foot muscles led to a reduction in the work generated at the ankle during landing (~16%) and jumping (~12%) tasks. This finding is consistent with our previous reports during constant-speed walking and running (Farris et al., 2019), and further highlights the functional coupling between the intrinsic foot muscles and ankle plantar flexor muscles. The underlying mechanism for the reduction in ankle joint work when the nerve block was in place is currently unknown. However, it may be explained via a shared neural drive (Kelly et al., 2018) or via mechanical coupling between the foot and ankle. When humans jump, the external moment arm to the ankle (GRF to ankle joint) is shortest at the bottom of a jump and increases throughout leg extension (Farris et al., 2016). We suspect that the nerve block, by removing activation of the intrinsic foot muscles, may interfere with this behavior by reducing the gear ratio of ankle plantarflexors, resulting in potentially faster shortening velocities. This would be akin to an inverse of stiffening the foot reported by Takahashi et al. (2016) and would serve as an explanation for observed reductions in both ankle work (see Tables 1 and 2) and mean ankle moments (see Figs S3 and S4). However, this remains speculation at this point.

Limitations

This study has several experimental limitations to discuss. First, our participants performed unilateral landings and jumps for our protocol, making our data difficult to compare with many existing studies, particularly in relation to joint contributions. This occurred as a result of a limited anesthetic dosage for the nerve block; to ensure a true comparison of foot and ankle contributions with and without intrinsic foot muscle activity, we chose to only apply the block to one foot. Participants were able to perform work on the COM by swinging their

non-jumping leg up when jumping, which may have affected the work contributions of the foot/leg under examination. In an attempt to deter this, vocal instruction was given prior to all jumping and throughout the protocol if the aforementioned strategy was noticed. During our landing protocol, participants tended to use their non-landing leg to lower the COM when stepping off of the boxes, thereby reducing the total amount of negative work needed to complete deceleration. A vocal cue of 'walking the plank' was given in attempts to remedy this, where participants were required to maintain full extension of the non-landing leg throughout the step-off. This way, the descent was initiated only when the COM fell outside of the base of support. It may have been beneficial for controlling the COM to employ a protocol similar to that used by Olsen et al. (2019), where the descent was initiated by releasing the grip from an overhead hanging position instead. Finally, all boxes used for our landing protocol were chosen based on their convenience of availability and assembly, as well as their ability to be assembled in relatively linear height graduations. Although we observed significant differences in negative COM work between our landing heights, we may have better controlled task performance by the construction of boxes allowing more variation in height. This would have allowed us to normalize the step height to potential energy instead of box height, as the latter allows differences in height to affect the magnitude of COM work between participants.

In conclusion, we have demonstrated that the foot and its intrinsic muscles can modulate their energetic function to match increasing work demands of the COM. The foot's motor and damping capacities revealed by our data and recent studies have potential implications for foot prosthetic and footwear design. Additionally, without the intrinsic foot muscles, both the foot and ankle's contributions to landing and jumping are diminished. As the ankle serves as a primary power producer in a number of locomotive modalities, the capacity for the foot to influence the ankle is noteworthy to future research examining movement energetics.

Acknowledgements

We thank Dr Sarah Kessler from Harvard University for her aid in data collection and data processing. We also thank Dr Andrew Cresswell from the University of Queensland for advice on data processing.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Methodology: G.A.L., L.A.K.; Investigation: R.E.S.; Data curation: R.E.S.; Writing - original draft: R.E.S.; Writing - review & editing: R.E.S., G.A.L., L.A.K.; Supervision: G.A.L., L.A.K.; Project administration: G.A.L., L.A.K.; Funding acquisition: L.A.K.

Funding

This work was funded by an Australian Research Council Linkage Grant (LP160101316), in collaboration with Asics Oceania and The Australian Sports Commission.

Data availability

A copy of the Matlab file containing all dependent variable data is available from the University of Queensland Research Data Manager: <https://rdm.uq.edu.au/record/PHDRS0824>

References

- Bennett, M. B. and Ker, R. F. (1990). The mechanical properties of the human subcalcaneal fat pad in compression. *J. Anat.* **171**, 131-138.
- Biewener, A. A. and Roberts, T. J. (2000). Muscle and tendon contributions to force, work, and elastic energy savings: a comparative perspective. *Exerc. Sport Sci. Rev.* **28**, 99-107.
- Daley, M. A. and Biewener, A. A. (2003). Muscle force-length dynamics during level versus incline locomotion: a comparison of in vivo performance of two guinea fowl ankle extensors. *J. Exp. Biol.* **206**, 2941-2958. doi:10.1242/jeb.00503
- Dempster, W. T. (1955). *Space Requirements of the Seated Operator: Geometrical, Kinematic, and Mechanical Aspects of the Body with Special Reference to the Limbs*. Ann Arbor, Michigan: University of Michigan.
- Derrick, T. R., van den Bogert, A. J., Cereatti, A., Dumas, R., Fantozzi, S. and Leardini, A. (2020). ISB recommendations on the reporting of intersegmental forces and moments during human motion analysis. *J. Biomech.* **99**, 109533. doi:10.1016/j.jbiomech.2019.109533
- Devita, P., Janshen, L., Rider, P., Solnik, S. and Hortobágyi, T. (2008). Muscle work is biased toward energy generation over dissipation in non-level running. *J. Biomech.* **41**, 3354-3359. doi:10.1016/j.jbiomech.2008.09.024
- Farris, D. J., Lichtwark, G. A., Brown, N. A. and Cresswell, A. G. (2016). The role of human ankle plantar flexor muscle-tendon interaction and architecture in maximal vertical jumping examined in vivo. *J. Exp. Biol.* **219**, 528-534. doi:10.1242/jeb.126854
- Farris, D. J., Kelly, L. A., Cresswell, A. G. and Lichtwark, G. A. (2019). The functional importance of human foot muscles for bipedal locomotion. *Proc. Natl. Acad. Sci. USA* **116**, 1645-1650. doi:10.1073/pnas.1812820116
- Hanavan, E. P. (1964). A mathematical model of the human body. *Aerospace Med. Res. Laboratories* **1964**, 1-149.
- Kelly, L. A., Cresswell, A. G., Racinais, S., Whiteley, R. and Lichtwark, G. (2014). Intrinsic foot muscles have the capacity to control deformation of the longitudinal arch. *J. R. Soc. Interface* **11**, 20131188. doi:10.1098/rsif.2013.1188
- Kelly, L. A., Lichtwark, G. and Cresswell, A. G. (2015). Active regulation of longitudinal arch compression and recoil during walking and running. *J. R. Soc. Interface* **12**, 20141076. doi:10.1098/rsif.2014.1076
- Kelly, L. A., Cresswell, A. G. and Farris, D. J. (2018). The energetic behaviour of the human foot across a range of running speeds. *Sci. Rep.* **8**, 10576. doi:10.1038/s41598-018-28946-1
- Ker, R. F., Bennett, M. B., Bibby, S. R., Kester, R. C. and Alexander, R. M. (1987). The spring in the arch of the human foot. *Nature* **325**, 147-149. doi:10.1038/325147a0
- Leardini, A., Benedetti, M. G., Berti, L., Bettinelli, D., Nativo, R. and Giannini, S. (2007). Rear-foot, mid-foot and fore-foot motion during the stance phase of gait. *Gait Posture* **25**, 453-462. doi:10.1016/j.gaitpost.2006.05.017
- Ledoux, W. R. and Blevins, J. J. (2007). The compressive material properties of the plantar soft tissue. *J. Biomech.* **40**, 2975-2981. doi:10.1016/j.jbiomech.2007.02.009
- Lu, T.-W. and O'Connor, J. J. (1999). Bone position estimation from skin marker coordinates using global optimisation with joint constraints. *J. Biomech.* **32**, 129-134. doi:10.1016/S0021-9290(98)00158-4
- Maharaj, J. N., Cresswell, A. G. and Lichtwark, G. A. (2017). Subtalar joint pronation and energy absorption requirements during walking are related to tibialis posterior tendinous tissue strain. *Sci. Rep.* **7**, 17958. doi:10.1038/s41598-017-17771-7
- Minetti, A. E., Ardigo, L. P. and Saibene, F. (1993). Mechanical determinants of gradient walking energetics in man. *J. Physiol.* **472**, 725-735. doi:10.1113/jphysiol.1993.sp019969
- Olsen, M. T., Bruening, D. A., Johnson, A. W. and Ridge, S. T. (2019). The role of the midfoot in drop landings. *Med. Sci. Sport Exerc.* **51**, 114-122. doi:10.1249/MSS.0000000000001765
- Orendurff, M. S., Schoen, J. A., Bernatz, G. C., Segal, A. D. and Klute, G. K. (2008). How humans walk: bout duration, steps per bout, and rest duration. *J. Rehabil. Res. Dev.* **45**, 1077-1090. doi:10.1682/JRRD.2007.11.0197
- Riddick, R., Farris, D. J. and Kelly, L. A. (2019). The foot is more than a spring: human foot muscles perform work to adapt to the energetic requirements of locomotion. *J. R. Soc. Interface* **16**, 20180680. doi:10.1098/rsif.2018.0680
- Sawicki, G. S., Lewis, C. L. and Ferris, D. P. (2009). It pays to have a spring in your step. *Exerc. Sport Sci. Rev.* **37**, 130-138. doi:10.1097/JES.0b013e31819c2df6
- Soo, C. H. and Donelan, J. M. (2012). Coordination of push-off and collision determine the mechanical work of step-to-step transitions when isolated from human walking. *Gait Posture* **35**, 292-297. doi:10.1016/j.gaitpost.2011.09.102
- Stearne, S. M., McDonald, K. A., Alderson, J. A., North, I., Oxnard, C. E. and Rubenson, J. (2016). The foot's arch and the energetics of human locomotion. *Sci. Rep.* **6**, 19403. doi:10.1038/srep19403
- Takahashi, K. Z., Kepple, T. M. and Stanhope, S. J. (2012). A unified deformable (UD) segment model for quantifying total power of anatomical and prosthetic below-knee structures during stance in gait. *J. Biomech.* **45**, 2662-2667. doi:10.1016/j.jbiomech.2012.08.017
- Takahashi, K. Z., Gross, M. T., van Werkhoven, H., Piazza, S. J. and Sawicki, G. S. (2016). Adding stiffness to the foot modulates soleus force-velocity behaviour during human walking. *Sci. Rep.* **6**, 29870. doi:10.1038/srep29870
- Takahashi, K. Z., Worster, K. and Bruening, D. A. (2017). Energy neutral: the human foot and ankle subsections combine to produce near zero net mechanical work during walking. *Sci. Rep.* **7**, 15404. doi:10.1038/s41598-017-15218-7
- Vanrenterghem, J., Lees, A., Lenoir, M., Aerts, P. and De Clercq, D. (2004). Performing the vertical jump: movement adaptations for submaximal jumping. *Hum. Mov. Sci.* **22**, 713-727. doi:10.1016/j.humov.2003.11.001

- Vanrenterghem, J., Bobbert, M. F., Casius, L. J. R. and De Clercq, D.** (2008). Is energy expenditure taken into account in human sub-maximal jumping? A simulation study. *J. Electromyogr. Kinesiol.* **18**, 108-115. doi:10.1016/j.jelekin.2006.09.006
- Wade, L., Lichtwark, G. and Farris, D. J.** (2018). Movement strategies for countermovement jumping are potentially influenced by elastic energy stored and released from tendons. *Sci. Rep.* **8**, 2300. doi:10.1038/s41598-018-20387-0
- Werkhausen, A., Albracht, K., Cronin, N. J., Meier, R., Bojsen-Møller, J. and Seynnes, O. R.** (2017). Modulation of muscle-tendon interaction in the human triceps surae during an energy dissipation task. *J. Exp. Biol.* **220**, 4141-4149. doi:10.1242/jeb.164111
- Yeow, C. H., Lee, P. V. and Goh, J. C.** (2011). An investigation of lower extremity energy dissipation strategies during single-leg and double-leg landing based on sagittal and frontal plane biomechanics. *Hum. Mov. Sci.* **30**, 624-635. doi:10.1016/j.humov.2010.11.010
- Zhang, S.-N., Bates, B. T. and Dufek, J. S.** (2000). Contributions of lower extremity joints to energy dissipation during landings. *Med. Sci. Sport Exerc.* **32**, 812-819. doi:10.1097/00005768-200004000-00014