

RESEARCH ARTICLE

Evaluating the ‘cost of generating force’ hypothesis across frequency in human running and hopping

Stephen P. Allen^{1,*}, Owen N. Beck² and Alena M. Grabowski^{1,3}

ABSTRACT

The volume of active muscle and duration of extensor muscle force well explain the associated metabolic energy expenditure across body mass and velocity during level-ground running and hopping. However, if these parameters fundamentally drive metabolic energy expenditure, then they should pertain to multiple modes of locomotion and provide a simple framework for relating biomechanics to metabolic energy expenditure in bouncing gaits. Therefore, we evaluated the ability of the ‘cost of generating force’ hypothesis to link biomechanics and metabolic energy expenditure during human running and hopping across step frequencies. We asked participants to run and hop at 85%, 92%, 100%, 108% and 115% of preferred running step frequency. We calculated changes in active muscle volume, duration of force production and metabolic energy expenditure. Overall, as step frequency increased, active muscle volume decreased as a result of postural changes via effective mechanical advantage (EMA) or duty factor. Accounting for changes in EMA and muscle volume better related to metabolic energy expenditure during running and hopping at different step frequencies than assuming a constant EMA and muscle volume. Thus, to ultimately develop muscle mechanics models that can explain metabolic energy expenditure across different modes of locomotion, we suggest more precise measures of muscle force production that include the effects of EMA.

KEY WORDS: Locomotion, Energetics, Biomechanics, Spring–mass model

INTRODUCTION

For decades, biomechanists and physiologists have sought to link the mechanics of running and hopping with the corresponding metabolic energy expenditure. One prevailing approach is the ‘cost of generating force’ hypothesis, which was proposed by Taylor and colleagues (Kram and Taylor, 1990; Taylor, 1994; Taylor et al., 1980) and posits that the primary determinant of the metabolic energy expenditure required for running and hopping is the cost of generating muscular force to support body weight. This hypothesis is predicated on the fact that animals produce stride-average vertical ground reaction forces equal to body weight when running or hopping on level ground. Previous studies have demonstrated that metabolic energy expenditure depends on animal size, and that

metabolic energy expenditure increases in almost direct proportion to the total weight of a running animal (Taylor et al., 1980). Further, per unit of body mass, it is more metabolically costly for smaller animals (e.g. mouse) to generate a unit of force than larger animals (e.g. horse) (Taylor, 1985), because small animals take more frequent strides and use less economical muscle fibers to produce force quickly (Heglund and Taylor, 1988). Thus, the metabolic energy expenditure during running and hopping varies with size and may depend on the number of strides taken per second, or stride frequency.

Kram and Taylor (1990) expanded the ‘cost of generating force’ hypothesis to explain why metabolic energy expenditure increases near linearly when running or hopping at faster velocities. They reasoned that the rate of force generation (i.e. the rate of cross-bridge cycling) could be approximated by the inverse of ground contact time and formally proposed that the rate of metabolic energy expenditure (\dot{E}_{met} in W) during running equals an animal’s body weight (F_{BW}) multiplied by the inverse of ground contact time (t_c^{-1}) and a metabolic cost coefficient (c) (Eqn 1):

$$\dot{E}_{\text{met}} = F_{\text{BW}} \cdot t_c^{-1} \cdot c. \quad (1)$$

To produce the force needed to support body weight over each stride, animals need to activate a volume of muscle (i.e. the number of active actin–myosin cross-bridges), which is primarily influenced by body weight and the leg’s effective mechanical advantage (EMA). EMA is the ratio of the ground reaction force moment arm to the muscle tendon moment arm. Kram and Taylor (1990) assumed that active muscle volume and EMA were independent of velocity (Biewener, 1989), which is why they simplified the equation to use force in units of body weight. Using this assumption, Eqn 1 well describes the increase in metabolic energy expenditure for a 10-fold increase in velocity and 4500-fold increase in body weight during forward hopping, trotting and running animals (Kram and Taylor, 1990; Roberts et al., 1998a).

Since Kram and Taylor (1990), multiple studies have shown that active muscle volume and EMA change across running velocity and limb morphology (Kipp et al., 2018b; Roberts et al., 1998b; Wright and Weyand, 2001). Notably, Roberts et al. (1998b) demonstrated that running bipeds have a greater EMA than size-matched quadrupeds as a result of their upright posture, which influences active muscle volume and metabolic energy expenditure. Thus, the authors proposed a refined version of the ‘cost of generating force’ hypothesis to account for changes in active muscle volume where the rate of metabolic energy expenditure equals the product of active muscle volume (V_m), the inverse of ground contact time and a new cost coefficient (k) (Eqn 2):

$$\dot{E}_{\text{met}} = V_m \cdot t_c^{-1} \cdot k. \quad (2)$$

Kipp et al. (2018b) applied this refined version of the ‘cost of generating force’ hypothesis (Eqn 2) to human running and found that humans decrease their EMA and increase active muscle volume

¹Department of Integrative Physiology, University of Colorado Boulder, Boulder, CO 80309, USA. ²The Wallace H. Coulter Department of Biomedical Engineering, Emory University and Georgia Institute of Technology, Atlanta, GA 30332, USA. ³Department of Veterans Affairs, Eastern Colorado Healthcare System, Denver, CO 80045, USA.

*Author for correspondence (stephen.allen-1@colorado.edu)

© S.P.A., 0000-0003-1599-7563; O.N.B., 0000-0003-0861-7163; A.M.G., 0000-0002-4432-618X

List of symbols and abbreviations

c	cost coefficient
EMA	effective mechanical advantage
\dot{E}_{met}	metabolic power
F_{BW}	force in units of body weight
F_{mtu}	muscle–tendon force
GRF	ground reaction force
k	cost coefficient
PSF	preferred step frequency
r	muscle–tendon moment arm
R	GRF moment arm
t_c	ground contact time
t_c^{-1}	rate of muscle force production
V_m	active muscle volume

by as much as 53% from 2.2 m s⁻¹ to 5.0 m s⁻¹. Thus, the authors concluded that the curvilinear increase in metabolic energy expenditure with running velocity (Batliner et al., 2018) results from an increase in active muscle volume and an increase in the rate of force production as a result of shorter ground contact times.

Though the rate of force generation and active muscle volume well explain metabolic energy expenditure across different running and hopping velocities, it is unknown whether these biomechanical variables adequately account for changes in metabolic energy expenditure across different stride and step frequencies, where during running, a step equals ground contact and the subsequent aerial time and two steps comprise a stride. Previous studies have shown that humans have a preferred step frequency when running at a constant velocity and hopping in place that minimizes metabolic energy expenditure, and deviating from the preferred step frequency increases metabolic energy expenditure (Allen and Grabowski, 2019; Cavagna et al., 1988; Cavanagh and Williams, 1982; Farris and Sawicki, 2012; Grabowski and Herr, 2009; Högberg, 1952; Raburn et al., 2011; Swinnen et al., 2021) – exhibiting a U-shaped relationship between metabolic energy expenditure and step frequency (Doke and Kuo, 2007; Snyder and Farley, 2011; Swinnen et al., 2021) under these conditions. Previous studies have suggested that the U-shaped relationship is due to simultaneous increasing and decreasing metabolic costs (Doke and Kuo, 2007; Snyder and Farley, 2011; Swinnen et al., 2021), where ground contact time decreases with increased step frequency during human running and hopping, which implies that humans must produce forces at a faster rate and increase metabolic cost (Farley et al., 1991). When considering the ‘cost of generating force’ hypothesis, Gutmann and Bertram (2017a,b) suggest that the rate of force production alone (Eqn 1) cannot fully account for the U-shaped changes in metabolic energy expenditure with hopping frequency, unless conditions are highly constrained (e.g. fixed hopping frequency and changing hop height), and may also depend on the cost of activating a given muscle volume. Therefore, accounting for changes in active muscle volume along with the rate of force production (Eqn 2) may better explain the U-shaped relationship between metabolic energy expenditure and step frequency. An increase in step frequency is simultaneously accompanied by shorter steps when running at a constant velocity, and a decrease in center of mass displacement during running and hopping – both of which may increase EMA, reduce active muscle volume and decrease metabolic cost (Monte et al., 2021). Thus, accounting for changes in the rate of force production and active muscle volume through EMA may better describe metabolic energy expenditure across step frequencies than the cost of generating force alone.

The purpose of this study was to determine how active muscle volume changes across step frequency in running and hopping, and to evaluate the ‘cost of generating force’ equations (Eqns 1 and 2), when changes in active muscle volume are accounted for. Both equations well characterize changes in metabolic energy expenditure across different velocities; however, accounting for changes in active muscle volume due to running and hopping mechanics may better account for the U-shaped changes in metabolic energy expenditure across different frequencies. We hypothesized that active muscle volume would decrease as step frequency increases in running and hopping as a result of increased EMA. Further, we hypothesized that accounting for changes in active muscle volume and the rate of force production (Eqn 2) would better explain changes in metabolic energy expenditure across step frequencies compared with the original ‘cost of generating force’ equation, which estimates active muscle volume from body weight (Eqn 1) for both running and hopping.

MATERIALS AND METHODS

Participants

Ten healthy runners (6 female, 4 male; mean±s.d. mass 60.7±8.9 kg, height 1.72±0.09 m, age 24.5±3.4 years) with no reported cardiovascular, neurological or musculoskeletal impairments participated in the study. All participants reported running for exercise at least 30 min per day, 3 times per week, for at least 6 months. Each participant provided written informed consent to participate in the study according to the University of Colorado Boulder Institutional Review Board.

Experimental protocol

Over two separate days, participants performed a series of running trials on a force-measuring treadmill (Treadmetrix, Park City, UT, USA; 1000 Hz) and stationary, two-legged hopping trials on force plates (Bertec, Columbus, OH, USA; 1000 Hz) while we simultaneously measured ground reaction forces, lower limb kinematics, and metabolic energy expenditure throughout each trial. On the first day, participants performed six, 5 min running trials at 3 m s⁻¹. During the first trial, we determined each participant’s preferred step frequency (PSF). We collected ground reaction forces (GRFs) for 15 s during the third and fifth minute of the first trial and determined average PSF from ground contact events identified by a 20 N vertical GRF threshold. We then instructed participants to complete the remaining running trials while matching their step frequency to the timing of an audible metronome. The metronome was set to 85%, 92%, 100%, 108% and 115% of their PSF, similar to previous studies (Snyder and Farley, 2011; Swinnen et al., 2021), and the order of the trials was randomized.

On the second day, participants performed five, 5 min stationary hopping trials, on both feet. To account for the effects of frequency on metabolic energy expenditure and given the similarity of frequencies that minimize metabolic energy expenditure during hopping and running (Allen and Grabowski, 2019; Cavagna et al., 1997; Farris and Sawicki, 2012; Grabowski and Herr, 2009; Kaneko et al., 1987), we instructed participants to hop in place while matching their step frequency to the audible metronome set to 85%, 92%, 100%, 108% and 115% of their PSF from day 1. The order of the hopping trials was randomized, and we did not determine preferred hopping frequency.

Metabolic energy expenditure

We measured participants’ rates of oxygen consumption and carbon dioxide production via indirect calorimetry (TrueOne 2400, ParvoMedics, Sandy, UT, USA) throughout each running and

hopping trial. We instructed participants to refrain from exercising before each experimental session or ingesting caffeine 4 h before each experimental session to minimize day-to-day variability in metabolic rate. Additionally, participants were instructed to be at least 2 h postprandial at the start of each experimental session to mitigate potential effects of diet on metabolic measurements. Further, each experimental session was performed at the same time each day and separated by at least 24 h to eliminate any potential effects of day-to-day variability or fatigue. We calculated gross steady-state metabolic power from the average metabolic rates during the last 2 min of each 5 min trial using a standard equation (Kipp et al., 2018a; Péronnet and Massicotte, 1991).

Kinematics and kinetics

We positioned 40 reflective markers bilaterally on both legs and the pelvis. Markers on the ankles and knees were used to define joint centers and clusters of 3–4 markers were placed on each segment prior to experimental trials. We collected lower limb kinematic data for 15 s during the last minute of each trial using 3D motion capture (Vicon Nexus 2.3, Oxford, UK; 200 Hz) simultaneously with GRFs. We analyzed 20 steps from each trial and used a 4th order low-pass Butterworth filter with a 20 Hz cut-off to process analog GRF signals and marker trajectories (Alcantara, 2019; Mai and Willwacher, 2019). We determined ground contact using a 20 N vertical GRF threshold for both running and hopping and calculated the rate of force production as the inverse of ground contact time (t_c^{-1}).

To calculate EMA and V_m , we estimated the average extensor muscle–tendon unit force (F_{mtu}) about each joint assuming a constant muscle–tendon moment arm (r) for each muscle group and using instantaneous ankle, knee and hip sagittal joint moments from

Visual 3D (Visual 3D, C-Motion Inc., Germantown, MD, USA) (Biewener et al., 2004; Kipp et al., 2018b). We only included joint moment values that exceeded 25% of the maximum extensor moment because of the inherently noisy center of pressure measurements caused by low force values at the beginning and end of the ground contact phase (Biewener et al., 2004; Griffin et al., 2003; Kipp et al., 2018b). Because the net joint moments of the knee and hip include flexion moments from bi-articular muscles, we accounted for forces in bi-articular muscles by assuming F_{mtu} was proportional to the physiological cross-sectional area of active muscle fibers (Eqns 3–5).

$$M_{\text{ankle}} = r_{\text{ankle}} \cdot F_{\text{mtu,ankle}}, \quad (3)$$

$$M_{\text{knee}} = r_{\text{knee}} \cdot F_{\text{mtu,knee}} - \left(r_{\text{BF}} \cdot F_{\text{mtu,hip}} \frac{\text{PCSA}_{\text{BF}}}{\sum \text{PCSA}_{\text{hip}}} \right) - \left(r_{\text{Gas}} \cdot F_{\text{mtu,ankle}} \frac{\text{PCSA}_{\text{Gas}}}{\sum \text{PCSA}_{\text{ankle}}} \right), \quad (4)$$

$$M_{\text{hip}} = r_{\text{hip}} \cdot F_{\text{mtu,hip}} - \left(r_{\text{RF}} \cdot F_{\text{mtu,knee}} \frac{\text{PCSA}_{\text{RF}}}{\sum \text{PCSA}_{\text{knee}}} \right), \quad (5)$$

where M is the net joint moment, r is a weighted-average muscle–tendon moment arm and PCSA is the physiological cross-sectional area. Gas, BF and RF represent the properties of the gastrocnemius, biceps femoris and rectus femoris muscles, respectively. We calculated $F_{\text{mtu,ankle}}$ from Eqn 3, and solved Eqns 4 and 5 simultaneously because of the two unknown quantities of $F_{\text{mtu,knee}}$ and $F_{\text{mtu,hip}}$. We considered moments that extend joints to be positive. Values for r and PCSA were taken from the anthropometric data of four male human cadavers reported in

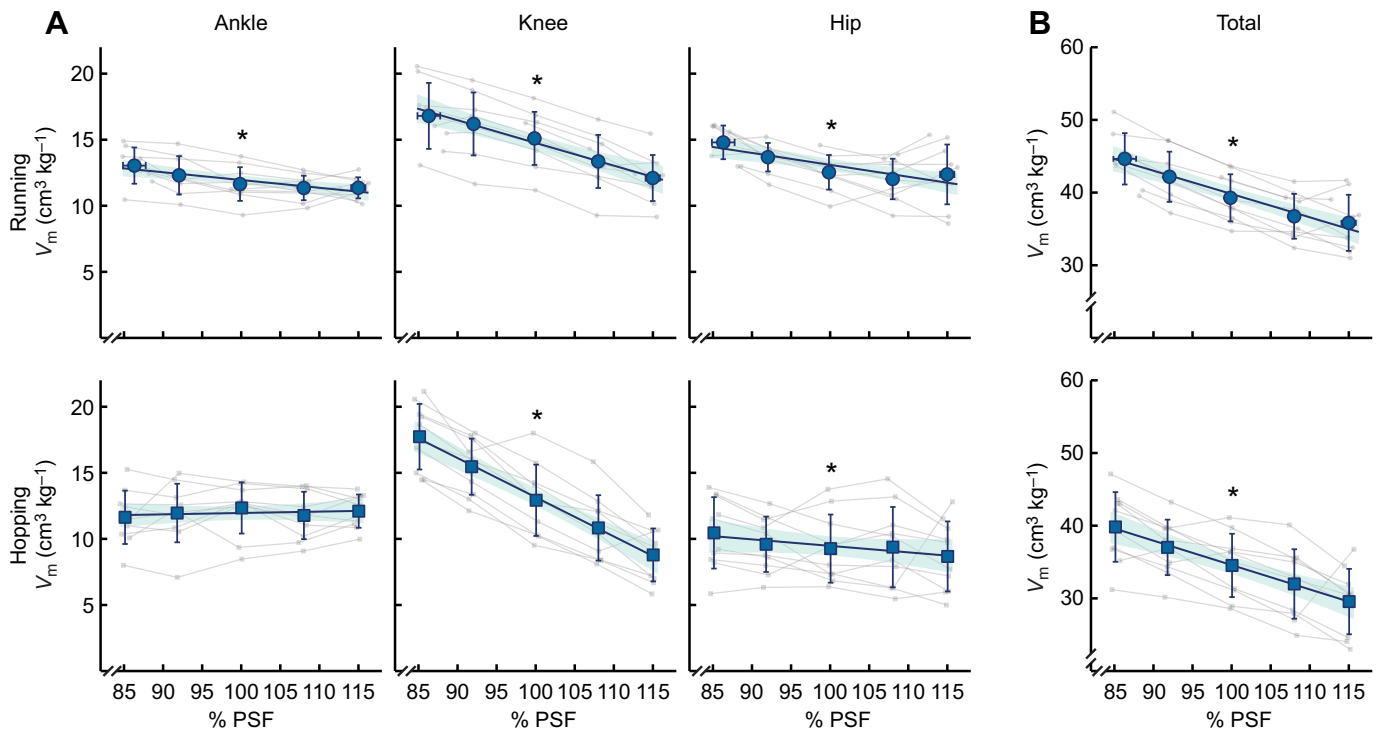


Fig. 1. Active muscle volume across percentage of preferred step frequency. Mean \pm s.d. active muscle volume (V_m) of the leg extensors during ground contact (blue symbols) and values from individual subjects (gray symbols) versus the percentage of running preferred step frequency (% PSF) for running and hopping. (A) V_m of the muscles surrounding the ankle, knee and hip joints during running (top) and hopping (bottom), and (B) the summed total of the ankle, knee and hip joint V_m . The dark lines represent the results of linear mixed-effects models, and the shaded regions represent the model's 95% confidence intervals. Coefficients and intercepts for each of the linear mixed-effects models are presented in Table 2. Asterisks indicate the model slope is significantly different from zero. Vertical and horizontal error bars may not be visible behind data points.

Table 1. Linear mixed-effects model results for effective mechanical advantage (Fig. 5) and active muscle volume (Fig. 4) at the ankle, knee and hip and the summed total while running and hopping at different percentages of preferred running step frequency

	Joint	V_m			EMA		
		Intercept	Slope	<i>P</i> -value	Intercept	Slope	<i>P</i> -value
Running	Ankle	17.6	-0.06	<0.001	0.32	-0.24×10^{-5}	0.87
	Knee	31.9	-0.17	<0.001	0.29	1.0×10^{-3}	0.07
	Hip	22.5	-0.09	<0.001	0.76	-4.9×10^{-4}	0.67
	Total	72.2	-0.32	<0.001	—	—	—
Hopping	Ankle	11.0	0.01	0.43	0.39	-3.6×10^{-4}	0.06
	Knee	42.7	-0.30	0.001	-0.40	8.4×10^{-3}	<0.001
	Hip	14.4	-0.05	0.0275	0.63	2.7×10^{-3}	0.35
	Total	68.1	-0.34	<0.001	—	—	—

Biewener et al. (2004) and previously used in Kipp et al. (2018b). We then used the quotient of the average sagittal plane resultant GRF magnitude and F_{mtu} at each joint during ground contact to calculate EMA, which equals the quotient of r and the GRF moment arm (R).

$$EMA = \frac{GRF}{F_{mtu}} = \frac{r}{R}. \quad (6)$$

We calculated V_m separately for each joint (Eqn 7) and then summed them to estimate the total average V_m per leg. To do this, we assumed the muscles produced force isometrically with a constant stress ($\sigma = 20 \text{ N cm}^{-2}$) (Perry et al., 1988) and combined this with our estimates of F_{mtu} and weighted-average fascicle length (L) from

Biewener et al. (2004):

$$V_m = \frac{F_{mtu} \cdot L}{\sigma}. \quad (7)$$

Estimating cost coefficients and metabolic energy expenditure

We calculated the metabolic cost coefficients, c and k , for each trial during running and hopping using Eqns 1 and 2. We averaged each cost coefficient across the range of frequencies (separately for running and hopping). Then we implemented the respective cost coefficient averages in addition to V_m , t_c^{-1} and F_{BW} to predict metabolic power for each step frequency during running and hopping using Eqns 1 and 2.

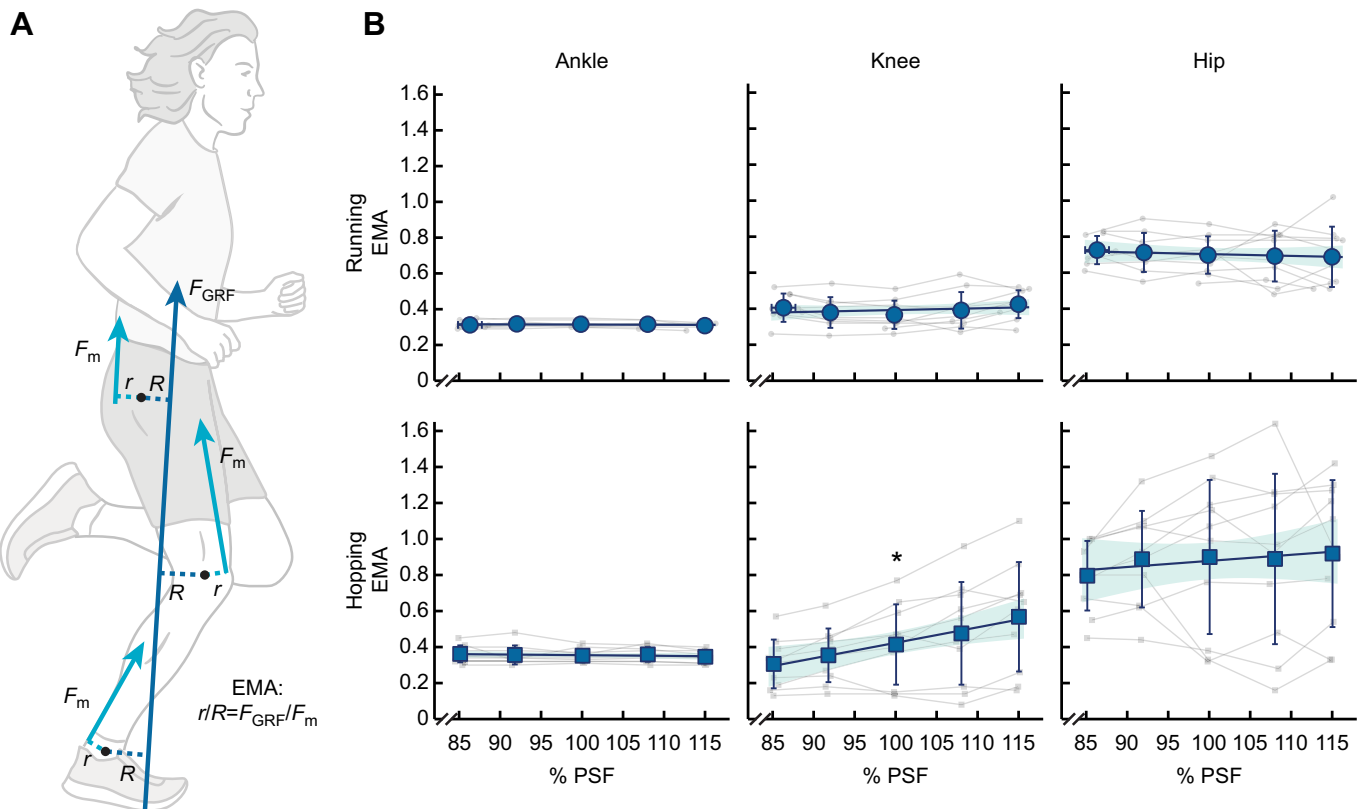


Fig. 2. Effective mechanical advantage (EMA) across percentage of PSF. (A) Illustration of EMA during running, which equals the ratio of the muscle–tendon moment arm (r) and the external resultant ground reaction force moment arm (R) or the ratio of resultant ground reaction force (F_{GRF}) and muscle force (F_m). (B) Mean \pm s.d. EMA for the ankle, knee and hip joints (blue symbols) with values for individual subjects (gray symbols) versus the percentage of running PSF. The dark lines represent the results of linear mixed-effects models and the shaded regions represent the model's 95% confidence intervals. Coefficients and intercepts for each of the linear mixed-effects models are presented in Table 2. Asterisks indicate the model slope is significantly different from zero. Vertical and horizontal error bars may not be visible behind data points.

Table 2. Biomechanical variables for running (3 m s⁻¹) and hopping in place at different percentages of preferred running step frequency

	Target % PSF	Achieved % PSF	Achieved step frequency (Hz)	Stance mean resultant GRF (BW)	Mean extension moment (N m kg ⁻¹)		
					Ankle	Knee	Hip
Running	85	86.3±1.5	2.50±0.10	1.60±0.12	2.35±0.25	1.77±0.37	1.06±0.13
	92	92.0±0.2	2.67±0.09	1.52±0.09	2.22±0.26	1.73±0.35	0.97±0.10
	100	100.0±0.1	2.90±0.11	1.42±0.09	2.10±0.23	1.62±0.29	0.88±0.12
	108	108.1±0.3	3.13±0.11	1.40±0.09	2.05±0.17	1.37±0.30	0.87±0.16
	115	115.2±0.5	3.34±0.13	1.36±0.13	2.05±0.14	1.17±0.23	0.93±0.21
Hopping	85	85.1±0.4	2.46±0.09	1.49±0.11	2.10±0.36	2.04±0.37	0.63±0.25
	92	91.8±0.3	2.66±0.09	1.47±0.08	2.16±0.40	1.71±0.33	0.59±0.20
	100	100.1±0.2	2.90±0.10	1.49±0.09	2.23±0.35	1.33±0.40	0.62±0.22
	108	108.1±0.2	3.13±0.11	1.46±0.05	2.12±0.32	1.02±0.35	0.67±0.26
	115	115.1±0.3	3.33±0.12	1.46±0.08	2.18±0.28	0.73±0.26	0.65±0.23

Data are means±s.d. PSF, preferred running step frequency; GRF, ground reaction force. Mean joint moment is defined when extension moments are greater than 25% of the peak joint moment.

Statistics

To evaluate the agreement between measured metabolic power and predicted metabolic power from Eqns 1 and 2, we performed limits of agreement analyses (Bland–Altman) for each target step frequency and calculated the systematic bias (mean differences) and 95% limits of agreement. In conjunction, we also provide the minimum detectable change (Dontje et al., 2018) for each model. We also constructed linear mixed-effects models ($\alpha=0.05$) to determine the effect of measured step frequency relative to PSF on t_c^{-1} , c , k , EMA, V_m , average joint extensor moment and average sagittal plane resultant GRF magnitude. In each linear mixed-effects model, we considered measured step frequency relative to PSF as a fixed effect and participant as a random effect. Model coefficients are reported alongside their P -values and represent the change in the dependent variable per a 1% change in measured step frequency relative to PSF. We performed all statistical analyses in R (version 3.6.3; <http://www.R-project.org/>) using custom scripts and packages (<https://github.com/deepankardatta/blandr/>; <https://CRAN.R-project.org/package=nlme>; <https://CRAN.R-project.org/package=psych>; <https://CRAN.R-project.org/package=ggplot2>).

RESULTS

We removed data for one participant at the 85% PSF and 92% PSF running trials because they were >3% off the target step frequencies.

Running

The linear mixed-effects model showed that total V_m decreased by 0.32 cm³ kg⁻¹ for every 1% increase in step frequency relative to PSF ($P<0.001$; Fig. 1B, Table 1). Specifically, participants decreased ankle, knee and hip V_m by 0.06, 0.17 and 0.09 cm³ kg⁻¹, respectively, for every 1% increase in step frequency ($P<0.001$ for each; Fig. 1A, Table 1). Despite the reduction in joint-specific V_m , we did not detect significant changes in ankle, knee or hip EMA across step frequency ($P=0.66$, $P=0.05$ and $P=0.59$, respectively). Mean (\pm s.d.) EMA across step frequencies for the ankle, knee and hip was 0.314±0.017, 0.393±0.084 and 0.714±0.117, respectively (Fig. 2, Table 1). Rather, the changes in joint-specific V_m may have been due to the decrease in average ankle, knee and hip extensor moments as step frequency increased. Average ankle, knee and hip extensor moments decreased by 0.01 N m kg⁻¹ ($P<0.001$), 0.02 N m kg⁻¹

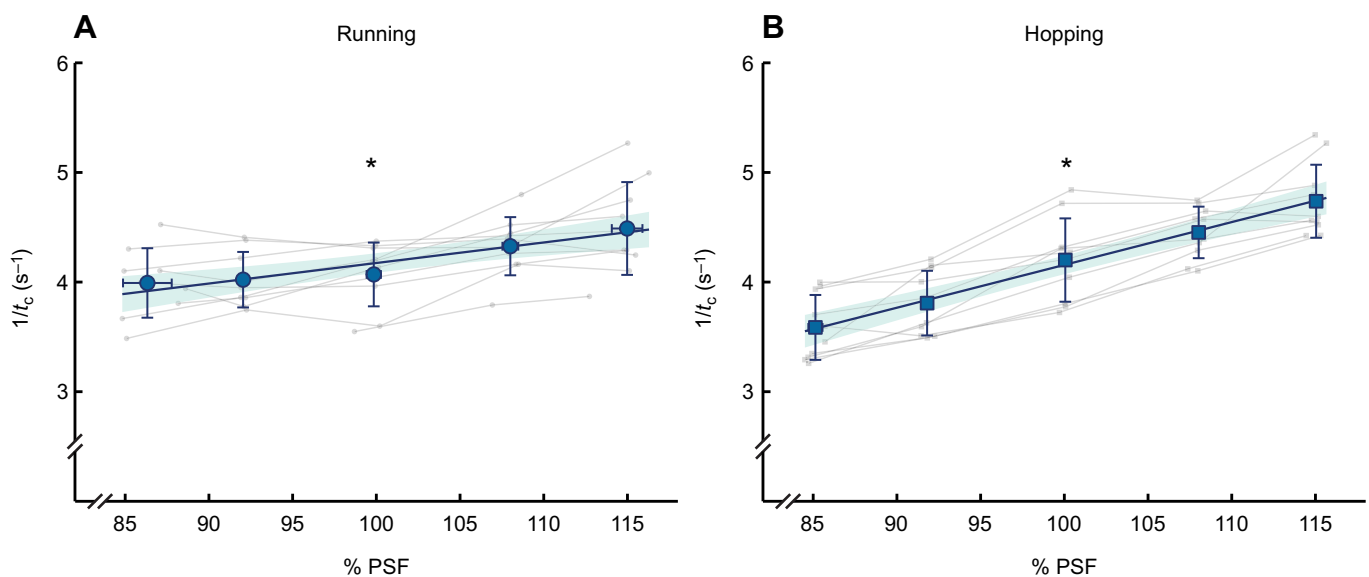


Fig. 3. Rate of force production across percentage of PSF. Mean±s.d. rate of force production (t_c^{-1} ; blue symbols) and values from individual subjects (gray symbols) versus the percentage of running PSF for (A) running and (B) hopping. The dark lines represent the model prediction across percentage of PSF (running: $t_c^{-1}=0.021\text{PSF}+2.160$, hopping: $t_c^{-1}=0.040\text{PSF}+0.216$) and the shaded areas represent the 95% confidence interval. Asterisks indicate the model slope is significantly different from zero. Vertical and horizontal error bars may not be visible behind data points.

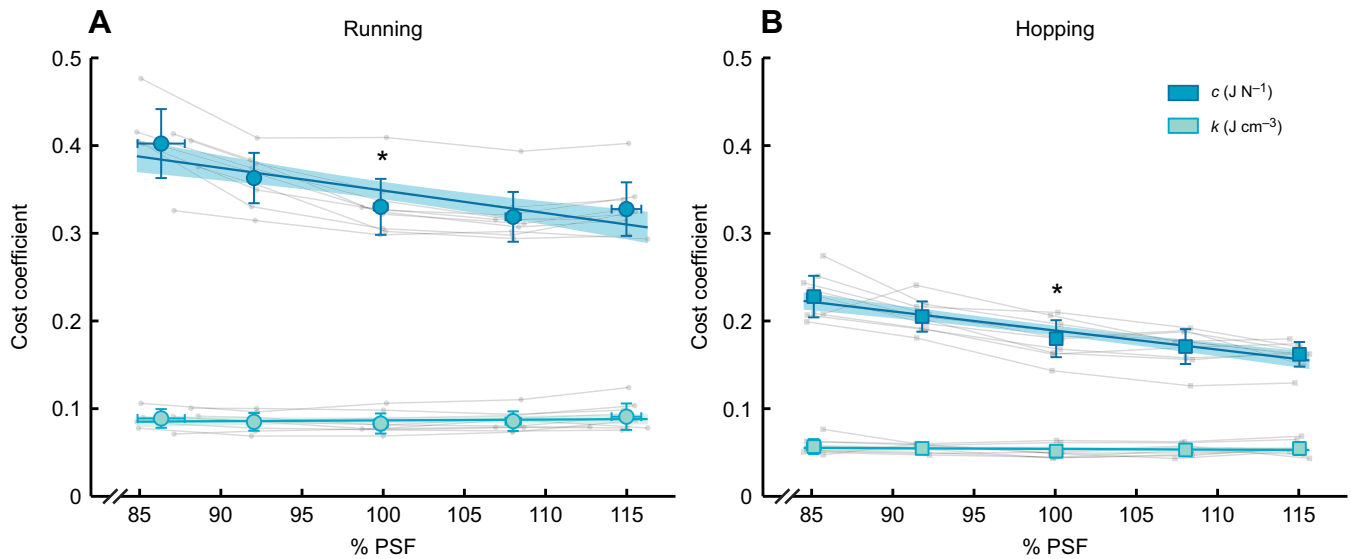


Fig. 4. Cost coefficient across percentage of PSF. Mean \pm s.d. cost coefficients (c – dark blue symbols; k – light blue symbols) and values from individual subjects (gray symbols) versus the percentage of running PSF in (A) running and (B) hopping. The lines represent the results of the linear mixed-effects model where $c = -0.003\text{PSF} + 0.601$ ($P < 0.001$) and $k = 1.16 \times 10^{-4}\text{PSF} + 0.075$ ($P = 0.18$) for running, and $c = -0.0022\text{PSF} + 0.407$ ($P < 0.001$) and $k = 0.001\text{PSF} + 0.045$ ($P = 0.20$) for hopping. Asterisks indicate the slope is significantly different from zero. The dark lines represent the results of linear mixed-effects models, and the shaded regions represent the model's 95% confidence intervals. Vertical and horizontal error bars may not be visible behind data points.

($P < 0.001$) and 0.01 N m kg^{-1} ($P = 0.002$), respectively, for every 1% increase in step frequency (Table 2). Finally, t_c^{-1} increased by 0.02 s^{-1} for every 1% increase in step frequency relative to PSF during running ($P < 0.001$; Fig. 3A). We used these variables to solve for the cost coefficient and found that c decreased by 0.003 J N^{-1} for every 1% increase in step frequency ($P < 0.001$; Fig. 4A), but k did not change across step frequency, and averaged (mean \pm s.d.) $0.087 \pm 0.003 \text{ J cm}^{-3}$ ($P = 0.18$; Fig. 4A).

On average, measured metabolic power was minimized when participants ran at their PSF (Fig. 5A), which was a mean (\pm s.d.) step frequency of $2.90 \pm 0.11 \text{ Hz}$ (Table 2). As participants deviated from their PSF, average measured metabolic power increased by

19% and 10% when running at 85% PSF and 115% PSF, respectively (Fig. 5A). Overall, metabolic power estimated with Eqn 1 underestimated average metabolic power for step frequencies slower than PSF (up to 13% at 85% PSF) but overestimated average metabolic power for step frequencies equal to or greater than PSF (up to 9% greater at 108% PSF) (Figs 6A,C and 7A). The limits of agreement analysis shows that the metabolic power estimated with Eqn 2 had a bias closer to zero and lower than Eqn 1 at each step frequency; however, the magnitude of the upper and lower limits of agreement for Eqn 2 was greater than that of Eqn 1 (Fig. 7A). The minimum detectable change was 3.1 W kg^{-1} and 3.8 W kg^{-1} using Eqns 1 and 2, respectively.

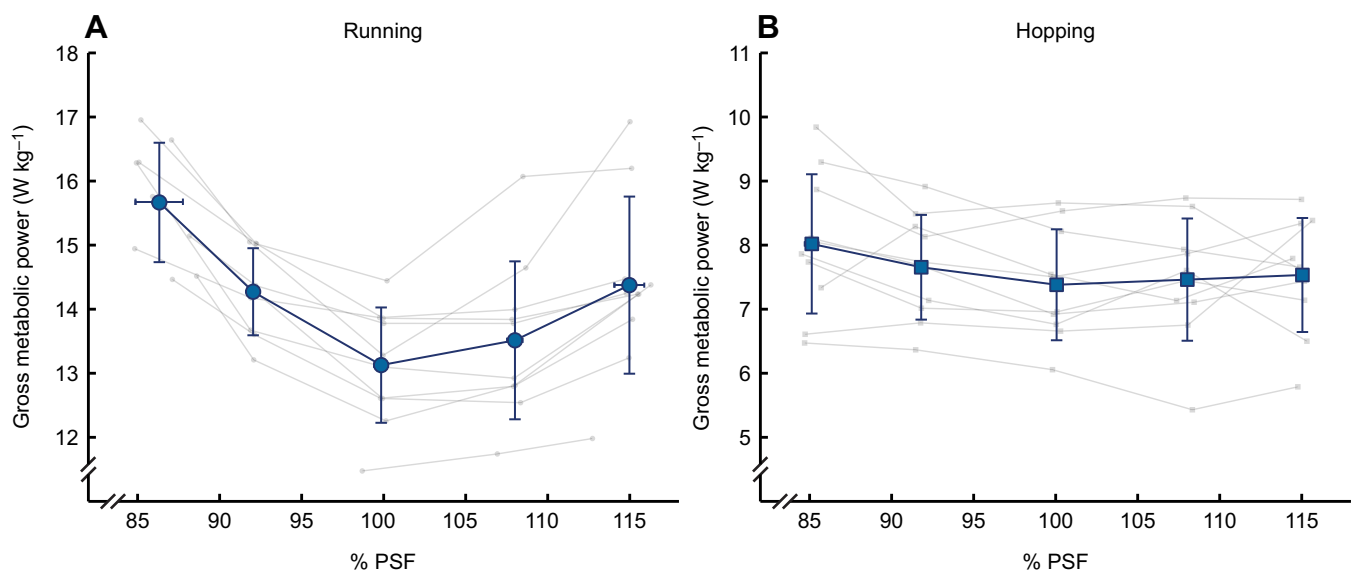


Fig. 5. Gross metabolic power across percentage of PSF. Mean \pm s.d. metabolic power (blue symbols) and values from individual subjects (gray symbols) versus the percentage of running PSF in (A) running and (B) hopping. Vertical and horizontal error bars may not be visible behind data points.

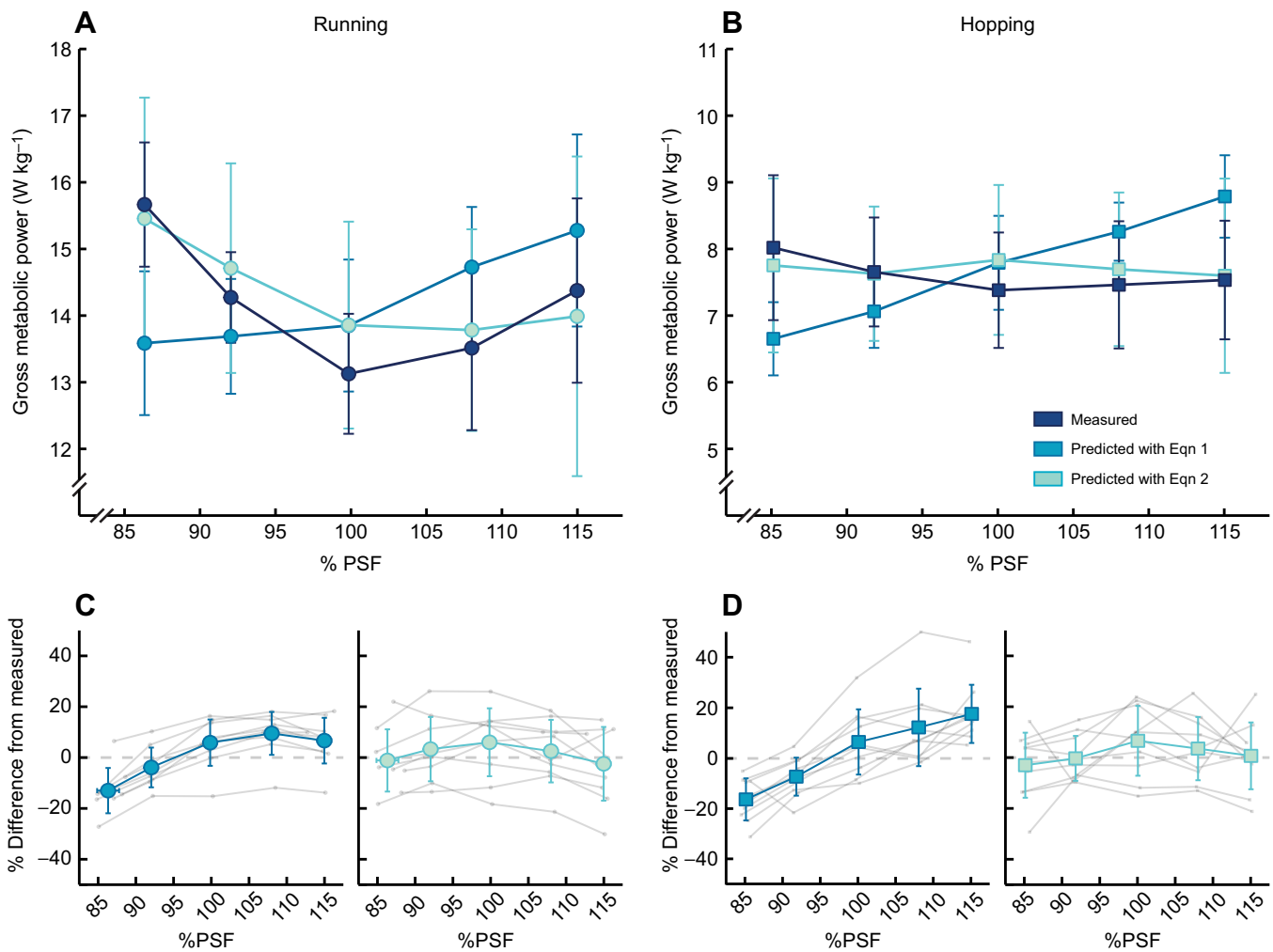


Fig. 6. Measured and predicted gross metabolic power across percentage of PSF. Mean \pm s.d. gross metabolic power for measured (dark blue) and predicted values using Eqn 1 (mid-blue) and Eqn 2 (light blue) versus the percentage of running PSF in (A) running and (B) hopping. Vertical and horizontal error bars may not be visible behind the data points. (C) Running and (D) hopping percentage difference between each equation and measured metabolic power for mean \pm s.d. values and individual subjects (gray symbols).

Hopping

The linear mixed-effects models showed that total V_m decreased by $0.34 \text{ cm}^3 \text{ kg}^{-1}$ for every 1% increase in step frequency relative to PSF ($P < 0.001$; Fig. 1B, Table 1). Participants decreased joint-specific V_m at the knee and hip by 0.30 and $0.05 \text{ cm}^3 \text{ kg}^{-1}$ for every 1% increase in step frequency ($P < 0.001$ and $P = 0.028$, respectively; Fig. 1A, Table 1), whereas ankle V_m did not change across step frequency and averaged (mean \pm s.d.) $11.96 \pm 1.81 \text{ cm}^3 \text{ kg}^{-1}$ ($P = 0.43$; Fig. 1A, Table 1). We found that knee EMA increased by 0.008 for every 1% increase in step frequency ($P < 0.001$; Fig. 2, Table 1). However, ankle and hip EMA did not change across step frequency, with a mean (\pm s.d.) of 0.35 ± 0.04 ($P = 0.06$) and 0.88 ± 0.36 ($P = 0.22$), respectively (Fig. 2, Table 1). Similarly, participants decreased average knee extensor moment by 0.04 N m kg^{-1} for every 1% increase in step frequency ($P < 0.001$; Table 2). However, average ankle and hip extensor moments did not change across step frequency and averaged (mean \pm s.d.) $2.16 \pm 0.33 \text{ N m}$ ($P = 0.43$) and $0.63 \pm 0.22 \text{ N m kg}^{-1}$ ($P = 0.34$), respectively. Finally, t_c^{-1} increased by 0.04 s^{-1} for every 1% increase in step frequency relative to PSF during stationary hopping ($P < 0.001$; Fig. 3B). We used these variables to solve for the cost coefficients and found that c decreased by 0.0022 J N^{-1} for every

1% increase in step frequency ($P < 0.001$; Fig. 4B), but k did not change across step frequency and averaged (mean \pm s.d.) $0.054 \pm 0.007 \text{ J cm}^{-3}$ ($P = 0.20$; Fig. 4B).

On average, measured metabolic power numerically increased by 9% and 2% when hopping at 85% PSF and 115% PSF, respectively, relative to 100% PSF ($P > 0.9$; Fig. 5B). On average, metabolic power estimated with Eqn 1 underestimated metabolic power for step frequencies slower than PSF (up to 17% at 85% PSF) but overestimated metabolic power for step frequencies greater than PSF (up to 17% at 115% PSF) (Figs 6B,D and 7B). Metabolic power estimated with Eqn 2 had a bias closer to zero and lower than Eqn 1 at each step frequency (Fig. 7B). The magnitude of the upper and lower limits of agreement for Eqn 2 were greater than those of Eqn 1 (Fig. 7B). The minimum detectable change was 2.6 and 2.1 W kg^{-1} using Eqns 1 and 2, respectively.

DISCUSSION

Our data partially support our first hypothesis as active muscle volume (V_m) per step decreased as step frequency increased when running at a constant velocity and hopping in place. When step frequency increased from 85% PSF to 115% PSF, we found that V_m

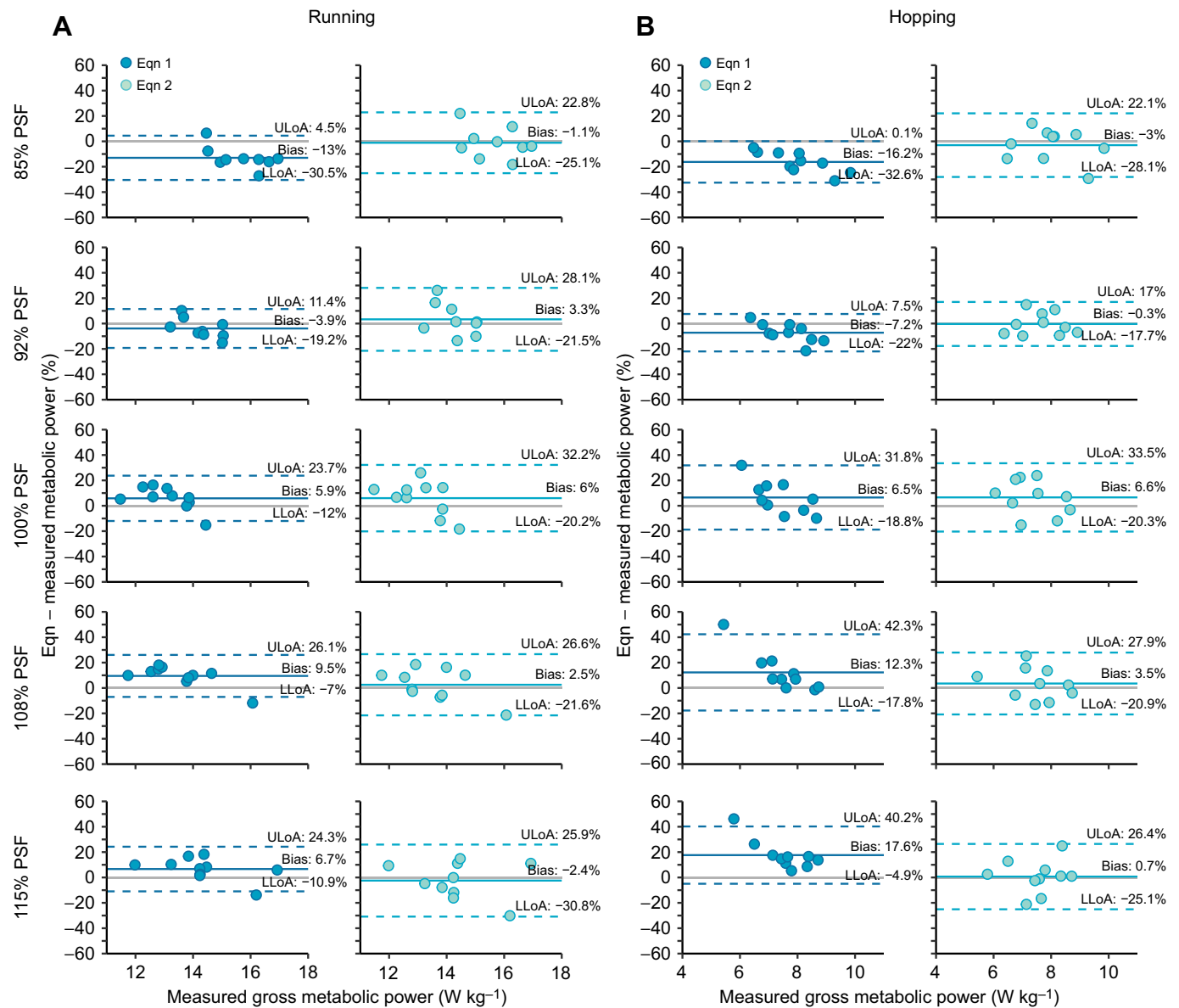


Fig. 7. Limits of agreement. Limits of agreement (Bland–Altman) analysis comparing the percentage difference between Eqn 1 (blue symbols) or Eqn 2 (light blue symbols) and gross metabolic power measured via indirect calorimetry. Mean differences (bias) are indicated by the solid colored lines, while the lower and upper limits of agreement (LLoA/ULoA) are denoted by dashed colored lines. LLoA/ULoA were calculated using 1.96 s.d.

decreased by 20% and 26% during running and hopping, respectively. This reduction predominantly occurred as a result of changes in V_m at the knee in both running and hopping, with smaller or non-significant contributions from the ankle and hip during both tasks (Fig. 1, Table 1). We found that the V_m at the knee accounted for ~53% and ~88% of the change in total V_m during running and hopping, respectively, whereas, when humans run at faster velocities from 2.2 to 5.0 m s⁻¹, V_m at the knee accounts for ~20% of the change in total active muscle volume (Kipp et al., 2018b).

The mechanism by which total V_m decreased with step frequency differed between running and hopping. We found that joint-specific EMA was independent of step frequency during running (Fig. 1, Table 1). Therefore, the reductions in total V_m during running were likely due to greater duty factors (product of contact time and frequency), which resulted in reduced stance-average resultant GRFs and the corresponding joint moments (Table 2). In comparison, during hopping, EMA at the knee increased by 86%

when step frequency increased from 85% to 115% PSF, while the magnitude of stance-average resultant GRF did not change (Fig. 2, Tables 1 and 2). This might imply that participants decreased total V_m during hopping by altering their lower limb position to hop with a straighter leg and extended knee as step frequency increased. When taken together, these results suggest that humans may utilize two different mechanisms to alter total V_m during bouncing gaits, duty factor (Beck et al., 2020) and EMA. Previously, Kipp et al. (2018b) demonstrated that humans utilize the two mechanisms simultaneously to increase total V_m when running at different velocities. They found that runners increased total V_m by 53% with faster running velocities from 2.2 to 5.0 m s⁻¹ as a result of a concurrent increase in GRFs and decrease in hip EMA, which is likely due to the increased step frequency that accompanies faster running velocity (Heglund and Taylor, 1988).

Our knee and ankle EMA results during two-legged, stationary hopping conflict with those of Monte et al. (2021), who suggest that

knee EMA is independent of step frequency (2.0–3.5 Hz). Our results may differ from those of Monte et al. (2021) because of a difference in methodology. We calculated joint-specific average EMA during the stance phase when joint moments exceeded 25% of their peak value, whereas Monte et al. (2021) separated stance into two phases and included EMA values obtained when GRF and center of pressure are noisy (near ground contact or toe off), which may increase variability in EMA and obscure changes that occur with step frequency (Griffin et al., 2003). There may have also been differences in inter-participant hopping strategies between studies, where participants adopt a strategy of hopping with their knees ‘locked’ or ‘unlocked’. While our average knee EMA data suggest that participants straightened their legs to hop at faster frequencies, three of our participants did not appreciably change their knee EMA across frequency (Fig. 2), which could be interpreted as choosing a ‘locked’ knee strategy.

Our results provide mixed support of our second hypothesis, that accounting for changes in V_m (Eqn 2) better explains changes in metabolic energy expenditure across step frequencies compared with the original ‘cost of generating force’ equation, which estimates V_m through body weight alone (Eqn 1). Eqn 1 exhibited a bias for running and hopping that systematically varied with step frequency – underestimating metabolic power for step frequencies lower than preferred and overestimating metabolic power for step frequencies higher than preferred (Fig. 7), which was likely due to the linear increase in the rate of force production (τ_c^{-1}). In contrast, Eqn 2 had a lower bias across all step frequencies for running and hopping, but wider limits of agreement (Fig. 7) that encompassed the average metabolic power between any two step frequencies. Additionally, the minimum detectable change for Eqns 1 and 2 was greater than the overall range of average measured metabolic power in running (2.6 W kg⁻¹) and hopping (0.6 W kg⁻¹). Together, these results might suggest that neither Eqn 1 or 2 is sensitive to the changes in metabolic power that occur with step frequency and they have limited usefulness when considering participant-specific responses. However, we found Eqn 2’s cost coefficient (k) to be near-constant across step frequency for running and hopping (Fig. 4), which suggests a better performing model because changes in metabolic power are proportional to changes in the rate of force produced and the total volume of active muscle (Griffin et al., 2003; Kipp et al., 2018a; Kram and Taylor, 1990; Roberts et al., 1998a,b). Thus, including changes in active muscle volume in the ‘cost of generating force’ equation may better account for changes in average metabolic power during running and hopping across different frequencies, but may require further refinement to be used to describe participant-specific responses.

Variation in the cost coefficient

The ‘cost of generating force’ hypothesis originally put forth by Kram and Taylor (1990) provides a simple equation (Eqn 1) that links biomechanics to metabolic energy expenditure across running velocities. However, this framework assumes animals employ a constant EMA, while muscles operate at consistent relative shortening velocities and lengths. Changes in the cost coefficient may result from differences in one of these assumptions (Full et al., 1990; Roberts et al., 1998a), whereas a constant cost coefficient implies that the primary mechanical determinants of metabolic energy expenditure have been accounted for. Here, we found that accounting for changes in V_m (Eqn 2) due to running or hopping mechanics results in a near-constant cost coefficient, k (Fig. 4), across step frequencies and is in line with previous research reported for human running (0.079 J cm⁻³) at different velocities (Kipp et al., 2018b).

Despite a near-constant cost coefficient while running and hopping at different step frequencies, the wide limits of agreement suggest that neither equation is sensitive to changes in metabolic energy expenditure, and this could be due to other factors that our study did not account for. For instance, Eqns 1 and 2 are not able to account for changes in the influence of muscle contractile dynamics (i.e. relative shortening velocity and fiber length) on metabolic energy expenditure. In a recent study, Beck et al. (2020) demonstrated that producing the same cycle-average force with a decreasing duty factor during cyclic soleus contractions requires greater peak muscle force, a decrease in fascicle operating length, and a general increase in active muscle volume and metabolic energy expenditure. Future studies might improve predictions of the ‘cost of generating force’ hypothesis by utilizing duty factor as a proxy for muscle contractile dynamics and validate it against ultrasound or modeling approaches.

In addition, although the ‘cost of generating force’ equations account for the majority of the metabolic cost of a muscle contraction, these equations are unable to account for 30–40% of the metabolic cost, which has been primarily attributed to ion pumping (Barclay, 2017; Rall, 1985) and cycling activating/deactivating muscles per unit time (Bergstrom and Hultman, 1988; Doke et al., 2005; Hogan et al., 1998). Cyclically activating and deactivating muscles at faster frequencies, such as in our study, should incur a large metabolic cost for ion pumping. Therefore, while these simple equations can be used to estimate metabolic energy expenditure in exercising animals, they do not fully account for all aspects of muscle metabolism that might be found in more detailed approaches (Umberger et al., 2003), and may contribute to variation in the cost coefficient and wide limits of agreement.

Running versus hopping

We evaluated how active muscle volume changes with step frequency during running and hopping, and how well changes in metabolic energy expenditure could be explained when accounting for these changes. We did not intend to compare running and hopping, yet it is interesting to note that the cost coefficient (k) is almost twice as large in running compared with hopping. One possible reason for this may be the metabolic cost of leg swing during running (Arellano and Kram, 2014; Doke et al., 2005; Marsh et al., 2004; Moed and Kram, 2005), which is estimated to comprise ~10–25% of the total metabolic cost of running, and is not accounted for in the ‘cost of generating force’ equation.

Previous research suggests that the metabolic cost surface of hopping (in the height–frequency domain) is different from that of running (Gutmann and Bertram, 2017b), where metabolic energy expenditure increases with hop height at a given frequency, likely as a result of an increase in the rate of force production and active muscle volume. Here, we did not constrain hop height in order to evaluate the ‘cost of generating force’ hypothesis on U-shaped metabolic energy expenditure data. However, future studies could determine how well these ‘cost of generating force’ equations predict metabolic cost when hopping frequency and height are constrained.

Limitations

A potential limitation of our study is the use of static internal muscle–tendon moment arms, fascicle lengths and pennation angles to estimate active muscle volume. We intentionally did this to allow a direct comparison of our results with those of previous studies

(Biewener et al., 2004; Kipp et al., 2018a) that account for active muscle volume changes during human locomotion. Previous studies have shown that muscle–tendon moment arms change with joint angle (Arnold et al., 2010; Hoy et al., 1990; Rasske et al., 2017). We found that accounting for active muscle volume increases inter-participant variability of predicted metabolic energy expenditure compared with assuming a constant active muscle volume (Figs 6 and 7). This increase in variability may be due to the assumption of fixed-length muscle moment arms. Inter-participant variability in total active muscle volume and predicted metabolic energy expenditure using Eqn 2 might be reduced by accounting for changes in muscle moment arms during the stance phase and/or scaling moment arms to leg lengths (Griffin et al., 2003). Thus, using variable muscle–tendon moment arms that change with joint angle could further improve the estimate of active muscle volume and metabolic energy expenditure during running and hopping.

Finally, we intentionally set out to investigate the changes in active muscle volume and evaluate the ‘cost of generating force’ equations when metabolic power demonstrates a U-shaped relationship with step frequency in two types of bouncing gaits – running and hopping. When running, this U-shaped relationship is observed at a constant velocity (Cavagna and Kaneko, 1977; Cavagna and Legramandi, 2015; Cavagna et al., 1997; Cavanagh and Williams, 1982; Heglund and Taylor, 1988; Högberg, 1952; Snyder and Farley, 2011; Swinnen et al., 2021); however, a change in step frequency is accompanied by a proportional change in step length. Therefore, we were unable to separate the effect of changing step frequency from step length and present the combined effects. Nonetheless, we provide information on the influence of changes in active muscle volume and the generalizability of a simple equation that relates metabolic energy expenditure to biomechanics.

Conclusion

In this study, we investigated changes in active muscle volume and evaluated the ‘cost of generating force’ hypothesis for predicting metabolic energy expenditure across different step frequencies during running and hopping. We found that accounting for changes in effective mechanical advantage to compute active muscle volume resulted in a near-constant cost coefficient, k , and may improve the estimation of average metabolic energy expenditure. Our data, along with previous studies, support the general hypothesis that the metabolic energy expenditure required for bouncing gaits is related to the magnitude of active muscle volume recruited to generate force and the rate that the force is produced, but further considerations of the model’s assumptions need to be addressed to further refine and account for variation in metabolic energy that occur with changes in step frequency.

Acknowledgements

We would like to acknowledge the members of the Applied Biomechanics Lab for their assistance with data collection.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.P.A., O.N.B., A.M.G.; Methodology: S.P.A., O.N.B., A.M.G.; Formal analysis: S.P.A.; Investigation: S.P.A., O.N.B.; Writing - original draft: S.P.A.; Writing - review & editing: S.P.A., O.N.B., A.M.G.; Visualization: S.P.A.; Supervision: A.M.G.

Funding

O.N.B. was supported by a Training Fellowship from the McCamish Parkinson’s Disease Innovation Program at Georgia Tech, Emory University.

References

- Alcantara, R. S.** (2019). Drift: a Python and MATLAB package to correct drifting ground reaction force signals during treadmill running. *J. Open Source Softw.* **4**, 1910. doi:10.21105/joss.01910
- Allen, S. P. and Grabowski, A. M.** (2019). Hopping with degenerative spring stiffness in a full-leg exoskeleton lowers metabolic cost compared with progressive spring stiffness and hopping without assistance. *J. Appl. Physiol.* **127**, 520–530. doi:10.1152/jappphysiol.01003.2018
- Arellano, C. J. and Kram, R.** (2014). Partitioning the metabolic cost of human running: a task-by-task approach. *Integr. Comp. Biol.* **54**, 1084–1098. doi:10.1093/icb/ucu033
- Arnold, E. M., Ward, S. R., Lieber, R. L. and Delp, S. L.** (2010). A model of the lower limb for analysis of human movement. *Ann. Biomed. Eng.* **38**, 269–279. doi:10.1007/s10439-009-9852-5
- Barclay, C. J.** (2017). Energy demand and supply in human skeletal muscle. *J. Muscle Res. Cell Motil.* **38**, 143–155. doi:10.1007/s10974-017-9467-7
- Batliner, M. E., Kipp, S., Grabowski, A. M., Kram, R. and Byrnes, W. C.** (2018). Does metabolic rate increase linearly with running speed in all distance runners? *Sports Med. Int. Open* **2**, E1–E8. doi:10.1055/s-0043-122068
- Beck, O. N., Gosyne, J., Franz, J. R. and Sawicki, G. S.** (2020). Cyclically producing the same average muscle–tendon force with a smaller duty increases metabolic rate. *Proc. R. Soc. B Biol. Sci.* **287**, 20200431. doi:10.1098/rspb.2020.0431
- Bergstrom, M. and Hultman, E.** (1988). Energy cost and fatigue during intermittent electrical stimulation of human skeletal muscle. *J. Appl. Physiol.* **65**, 1500–1505. doi:10.1152/jappl.1988.65.4.1500
- Biewener, A. A.** (1989). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**, 45–48. doi:10.1126/science.2740914
- Biewener, A., Farley, C. T., Roberts, T. J. and Termaner, M.** (2004). Muscle mechanical advantage of human walking and running: implications for energy cost. *J. Appl. Physiol.* **97**, 2266–2274. doi:10.1152/jappphysiol.00003.2004
- Cavagna, G. A. and Kaneko, M.** (1977). Mechanical work and efficiency in level walking and running. *J. Physiol.* **268**, 467–481. doi:10.1113/jphysiol.1977.sp011866
- Cavagna, G. A. and Legramandi, M. A.** (2015). Running, hopping and trotting: tuning step frequency to the resonant frequency of the bouncing system favors larger animals. *J. Exp. Biol.* **218**, 3276–3283. doi:10.1242/jeb.127142
- Cavagna, G. A., Franzetti, P., Heglund, N. C. and Willems, P.** (1988). The determinants of the step frequency in running, trotting and hopping in man and other vertebrates. *J. Physiol.* **399**, 81–92. doi:10.1113/jphysiol.1988.sp017069
- Cavagna, G. A., Mantovani, M., Willems, P. A. and Musch, G.** (1997). The resonant step frequency in human running. *Pflüg. Arch. Eur. J. Physiol.* **434**, 678–684. doi:10.1007/s004240050451
- Cavanagh, P. R. and Williams, K. R.** (1982). The effect of stride length variation on oxygen uptake during distance running. *Med. Sci. Sports Exerc.* **14**, 30–35. doi:10.1249/00005768-198201000-00006
- Doke, J. and Kuo, A. D.** (2007). Energetic cost of producing cyclic muscle force, rather than work, to swing the human leg. *J. Exp. Biol.* **210**, 2390–2398. doi:10.1242/jeb.02782
- Doke, J., Donelan, J. M. and Kuo, A. D.** (2005). Mechanics and energetics of swinging the human leg. *J. Exp. Biol.* **208**, 439–445. doi:10.1242/jeb.01408
- Dontje, M. L., Dall, P. M., Skelton, D. A., Gill, J. M. R. and Chastin, S. F. M. and Team, on behalf of the S. U.** (2018). Reliability, minimal detectable change and responsiveness to change: indicators to select the best method to measure sedentary behaviour in older adults in different study designs. *PLoS One* **13**, e0195424. doi:10.1371/journal.pone.0195424
- Farley, C. T., Blickhan, R., Saito, J. and Taylor, R. C.** (1991). Hopping frequency in humans: a test of how springs set stride frequency in bouncing gaits. *J. Appl. Physiol.* **1985**, 2127–2132. doi:10.1152/jappl.1991.71.6.2127
- Farris, D. J. and Sawicki, G. S.** (2012). Linking the mechanics and energetics of hopping with elastic ankle exoskeletons. *J. Appl. Physiol.* **113**, 1862–1872. doi:10.1152/jappphysiol.00802.2012
- Full, R. J., Zuccarello, D. A. and Tullis, A.** (1990). Effect of variation in form on the cost of terrestrial locomotion. *J. Exp. Biol.* **150**, 233–246. doi:10.1242/jeb.150.1.233
- Grabowski, A. M. and Herr, H. M.** (2009). Leg exoskeleton reduces the metabolic cost of human hopping. *J. Appl. Physiol.* **107**, 670–678. doi:10.1152/jappphysiol.91609.2008
- Griffin, T. M., Roberts, T. J. and Kram, R.** (2003). Metabolic cost of generating muscular force in human walking: insights from load-carrying and speed experiments. *J. Appl. Physiol.* **95**, 172–183. doi:10.1152/jappphysiol.00944.2002
- Gutmann, A. K. and Bertram, J. E. A.** (2017a). The apparently contradictory energetics of hopping and running: the counter-intuitive effect of constraints resolves the paradox. *J. Exp. Biol.* **220**, 167–170. doi:10.1242/jeb.144832
- Gutmann, A. K. and Bertram, J. E. A.** (2017b). Metabolic cost of human hopping. *J. Exp. Biol.* **220**, 1654–1662. doi:10.1242/jeb.150284

- Heglund, N. C. and Taylor, C. R.** (1988). Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* **138**, 301-318. doi:10.1242/jeb.138.1.301
- Hogan, M. C., Ingham, E. and Kurdak, S. S.** (1998). Contraction duration affects metabolic energy cost and fatigue in skeletal muscle. *Am. J. Physiol. Endocrinol. Metab.* **274**, E397-E402. doi:10.1152/ajpendo.1998.274.3.E397
- Hoy, M. G., Zajac, F. E. and Gordon, M. E.** (1990). A musculoskeletal model of the human lower extremity: the effect of muscle, tendon, and moment arm on the moment-angle relationship of musculotendon actuators at the hip, knee, and ankle. *J. Biomech.* **23**, 157-169. doi:10.1016/0021-9290(90)90349-8
- Högberg, P.** (1952). How do stride length and stride frequency influence the energy-output during running. *Arbeitsphysiologie* **14**, 437-441.
- Kaneko, K., Matsumoto, M., Ito, A. and Fuchimoto, T.** (1987). Optimum step frequency in constant speed running. In *Biomechanics X-B* (ed. B. Johnson), pp. 803-807. Champaign, IL: Human Kinetics.
- Kipp, S., Byrnes, W. C. and Kram, R.** (2018a). Calculating metabolic energy expenditure across a wide range of exercise intensities: the equation matters. *Appl. Physiol. Nutr. Metab.* **43**, 639-642. doi:10.1139/apnm-2017-0781
- Kipp, S., Grabowski, A. M. and Kram, R.** (2018b). What determines the metabolic cost of human running across a wide range of velocities? *J. Exp. Biol.* **221**, jeb184218. doi:10.1242/jeb.184218
- Kram, R. and Taylor, C. R.** (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267. doi:10.1038/346265a0
- Mai, P. and Willwacher, S.** (2019). Effects of low-pass filter combinations on lower extremity joint moments in distance running. *J. Biomech.* **95**, 109311. doi:10.1016/j.jbiomech.2019.08.005
- Marsh, R. L., Ellerby, D. J., Carr, J. A., Henry, H. T. and Buchanan, C. I.** (2004). Partitioning the energetics of walking and running: swinging the limbs is expensive. *Science* **303**, 80-83. doi:10.1126/science.1090704
- Moed, B. and Kram, R.** (2005). *Metabolic Costs of Forward Propulsion and Leg Swing at Different Running Speeds*. ISB XXth Congress - ASB 29th Annual Meeting July 31 - August 5, Cleveland, OH.
- Monte, A., Nardello, F. and Zamparo, P.** (2021). Mechanical advantage and joint function of the lower limb during hopping at different frequencies. *J. Biomech.* **118**, 110294. doi:10.1016/j.jbiomech.2021.110294
- Péronnet, F. and Massicotte, D.** (1991). Table of nonprotein respiratory quotient: an update. *Can. J. Sport Sci.* **16**, 23-29.
- Perry, A. K., Blickhan, R., Biewener, A. A., Heglund, N. C. and Taylor, R. C.** (1988). Preferred speeds in terrestrial vertebrates: are they equivalent? *J. Exp. Biol.* **137**, 207-219. doi:10.1242/jeb.137.1.207
- Raburn, C. E., Merritt, K. J. and Dean, J. C.** (2011). Preferred movement patterns during a simple bouncing task. *J. Exp. Biol.* **214**, 3768-3774. doi:10.1242/jeb.058743
- Rall, J. A.** (1985). Energetic aspects of skeletal muscle contraction: implications of fiber types. *Exerc. Sport Sci. Rev.* **13**, 33-74.
- Rasske, K., Thelen, D. G. and Franz, J. R.** (2017). Variation in the human Achilles tendon moment arm during walking. *Comput. Methods Biomech. Biomed. Eng.* **20**, 201-205. doi:10.1080/10255842.2016.1213818
- Roberts, T. J., Kram, R., Weyand, P. G. and Taylor, C. R.** (1998a). Energetics of bipedal running I. Metabolic cost of generating force. *J. Exp. Biol.* **201**, 2745-2751. doi:10.1242/jeb.201.19.2745
- Roberts, T. J., Chen, M. S. and Taylor, C. R.** (1998b). Energetics of bipedal running II. Limb design and running mechanics. *J. Exp. Biol.* **201**, 2753-2762. doi:10.1242/jeb.201.19.2753
- Snyder, K. L. and Farley, C. T.** (2011). Energetically optimal stride frequency in running: the effects of incline and decline. *J. Exp. Biol.* **214**, 2089-2095. doi:10.1242/jeb.053157
- Swinnen, W., Mylle, I., Hoogkamer, W., De Groot, F. and Vanwanseele, B.** (2021). Changing stride frequency alters average joint power and power distributions during ground contact and leg swing in running. *Med. Sci. Sports Exerc.* **53**, 2111-2118. doi:10.1249/MSS.0000000000002692
- Taylor, C. R.** (1985). Force development during sustained locomotion: a determinant of gait, speed and metabolic power. *J. Exp. Biol.* **115**, 253-262. doi:10.1242/jeb.115.1.253
- Taylor, C. R.** (1994). Relating mechanics and energetics during exercise. *Adv. Vet. Sci. Comp. Med.* **38A**, 181-215.
- Taylor, C. R., Heglund, N. C., McMahon, T. A. and Looney, T. R.** (1980). Energetic cost of generating muscular force during running. *J. Exp. Biol.* **86**, 9-18. doi:10.1242/jeb.86.1.9
- Umberger, B. R., Gerritsen, K. G. M. and Martin, P. E.** (2003). A Model of Human Muscle Energy Expenditure. *Comput. Methods Biomech. Biomed. Eng.* **6**, 99-111. doi:10.1080/1025584031000091678
- Wright, S. and Weyand, P. G.** (2001). The application of ground force explains the energetic cost of running backward and forward. *J. Exp. Biol.* **204**, 1805-1815. doi:10.1242/jeb.204.10.1805