



# Step time asymmetry increases metabolic energy expenditure during running

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## Abstract

To improve locomotor performance, coaches and clinicians encourage individuals with unilateral physical impairments to minimize biomechanical asymmetries. Yet, it is unknown if biomechanical asymmetries *per se*, affect metabolic energy expenditure in individuals with or without unilateral impairments during running. Thus, inter-leg biomechanical asymmetries may or may not influence distance-running performance. Purpose: We sought to determine whether running with asymmetric step times affects metabolic rate in unimpaired individuals. Methods: Ten unimpaired individuals were instructed to run on a force-measuring treadmill at 2.8 m/s and contact the ground simultaneously to the beat of an audible metronome. The metronome either played at time intervals equal to the respective participant's preferred step times (0% asymmetry), or at time intervals that elicited asymmetric step times between legs (7, 14, and 21% step time asymmetry); stride time remained constant across all trials. We measured ground reaction forces and metabolic rates during each trial. Results: Every 10% increase in step time and stance average vertical ground reaction force asymmetry increased net metabolic power by 3.5%. Every 10% increase in ground contact time asymmetry increased net metabolic power by 7.8%. More asymmetric peak braking and peak propulsive ground reaction forces, leg stiffness, as well as positive and negative external mechanical work, but not peak vertical ground reaction force, increased net metabolic power during running. Step time asymmetry increases the net metabolic power of unimpaired individuals during running. Therefore, unimpaired individuals likely optimize distance-running performance by using symmetric step times and overall symmetric biomechanics.

**Keywords** Symmetry · Economy · Biomechanics · Kinematics · Kinetics

## Abbreviations

BV Biomechanical variable  
GRF Ground reaction force  
Hz Hertz  
kg Kilogram  
m Meter

m/s Meters per second  
N Newton  
RER Respiratory exchange ratio  
SD Standard deviation  
SI Symmetry index  
VO<sub>2</sub> Rate of oxygen consumption  
VCO<sub>2</sub> Rate of carbon dioxide production  
W Watt

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## Introduction

During running, unimpaired individuals adopt symmetric inter-leg biomechanics. As such, many studies record biomechanical variables from both legs and only report the average between legs (Farley and González 1996; Grabowski and Kram 2008; Weyand et al. 2010). Similarly, some studies record single leg biomechanics and assume that the contralateral leg exhibits identical biomechanics (Cavanagh and Lafortune 1980). Furthermore, the fundamental movements

of running are well described via simple models that assume inter-leg symmetry (Blickhan 1989; McMahon and Cheng 1990; Morin et al. 2005; Weyand et al. 2000). Although running biomechanics are generally symmetric, a few studies indicate that unimpaired individuals adopt slight biomechanical asymmetries (Belli et al. 1995; Cavanagh et al. 1977; Furlong and Egginton 2018; Korhonen et al. 2010; Seminati et al. 2013; Zifchock et al. 2006). For example, during running at 3.7 m/s, Zifchock et al. (2006) reported that peak vertical ground reaction force (GRF) asymmetry is  $3.1 \pm 2.5\%$  (mean  $\pm$  SD; as per the symmetry index, see Eq. 1). Yet, issues in separating leg conditions (e.g., left versus right, kicking versus non-kicking, jumping versus non-jumping) (Korhonen et al. 2010; Munro et al. 1987) along with inconsistent asymmetry results (Belli et al. 1995; Cavanagh and Lafortune 1980; Cavanagh et al. 1977; Furlong and Egginton 2018; Korhonen et al. 2010; Seminati et al. 2013; Zifchock et al. 2006) suggest that individual variability may yield slight biomechanical asymmetries; however, as a cohort, unimpaired individuals use symmetric running biomechanics.

Many individuals with unilateral impairments exhibit asymmetric biomechanics. Namely, individuals with pathology (Böhm and Döderlein 2012), with a unilateral injury (Daly et al. 2016; Russell Esposito et al. 2015) or amputation (Beck et al. 2017; Grabowski et al. 2010; McGowan et al. 2012) typically adopt asymmetric running biomechanics. For instance, athletes with unilateral transtibial amputations exhibit 9% lower stance average vertical GRFs with their affected leg than their unaffected leg across a wide range of running speeds (3 m/s—top speed) (Grabowski et al. 2010). Due to the notion that asymmetric biomechanics cause inherently uneconomical locomotion (increased rates of metabolic energy expenditure during walking, running, etc.) (Cavanagh et al. 1977; Ellis et al. 2013; Jeffers and Grabowski 2017), many scientists, clinicians, coaches, and athletes aim to mitigate human biomechanical asymmetries through rehabilitation strategies, which include training interventions (Reisman et al. 2013, 2007; Wall and Turnbull 1986) and/or the use of assistive devices (Awad et al. 2017; Beck et al. 2017; Mattes et al. 2000; Russell Esposito et al. 2015).

Yet, it is unestablished whether biomechanical asymmetries per se, affect the rate of metabolic energy expenditure during running in unimpaired individuals. Currently, two studies with cross-sectional designs report conflicting results as to whether individuals who use relatively asymmetric running biomechanics yield increased (Cavanagh et al. 1977) or similar (Seminati et al. 2013) rates of metabolic energy expenditure compared to more symmetric individuals. Hence, a repeated-measures study design is warranted to establish whether asymmetric biomechanics affect metabolic energy expenditure during running.

The purpose of this study is to determine how asymmetric running biomechanics affect the rate of metabolic energy expenditure in unimpaired individuals. While controlling for covariates, reducing the rate of metabolic energy expended at a given running velocity elicits improved distance-running performance (Fuller et al. 2016; Hoogkamer et al. 2016; Joyner 1991). Unimpaired individuals naturally adopt step times that minimize their metabolic energy expenditure during running (Cavanagh and Williams 1982; Högberg 1952; Snyder and Farley 2011). Altered step time modulates the runner's ground contact times, GRFs, and spring-like biomechanics (Farley and González 1996; Morin et al. 2007). Altered ground contact time changes the allotted duration that muscles have to generate force to support body weight over each step (Kram 2000; Kram and Taylor 1990). Thus, reduced ground contact time requires muscles to generate force and support body weight over briefer durations, incurring faster rates of ATP utilization (Rall 1985). Exerting more force on the ground during running generally requires more active muscle volume, thereby increasing metabolic rate (Arellano and Kram 2014; Chang and Kram 1999). Further, altering spring-like running mechanics or positive external mechanical work, likely changes muscle mechanical work during running, thereby altering metabolic rates (Biewener and Roberts 2000; Cavagna and Kaneko 1977; Farley and González 1996; Morin et al. 2007; Ortega et al. 2015). Accordingly, we predict that varying step time asymmetry will change the metabolic rates of unimpaired individuals during running. Specifically, we hypothesized that increased step time asymmetry in unimpaired individuals would increase net metabolic power during running.

## Methods

### Participants

Ten individuals without apparent physical impairments (6 male/4 female; age:  $22.9 \pm 6.2$  years; mass:  $65.5 \pm 4.9$  kg; height  $1.71 \pm 0.05$  m; leg length:  $0.90 \pm 0.03$  m; average  $\pm$  SD) volunteered. Each participant ran for exercise at least three times per week for a minimum of 30 min per session over the preceding six months, and reported that they were free of neurological, orthopedic, and cardiovascular disorders. Prior to participation, we informed each individual of the benefits and risks involved with the study, and he/she gave written informed consent in accordance with the University of Colorado Institutional Review Board.

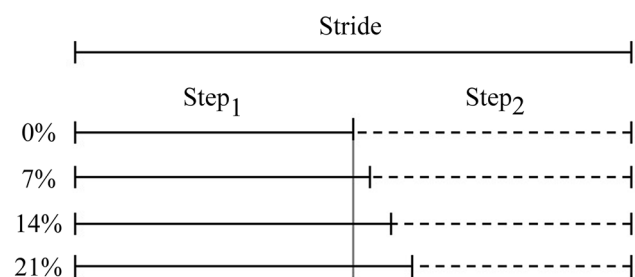
### Protocol

Each participant completed two identical testing sessions that were separated by at least 22 h. During each session,

participants began with a five-minute standing trial, followed by a set of seven running trials on a force-instrumented treadmill (Treadmetrix, Park City, UT, USA). All running trials were performed at 2.8 m/s and were followed with at least 5 min of rest. The first running trial lasted 12 min with the initial 11 min serving as familiarization to treadmill running. Over minute 12, we recorded GRFs during 30 consecutive seconds to establish each leg's preferred step time, where step time equals ground contact time plus the subsequent aerial time (Grabowski et al. 2010); two steps comprise a stride (Cavanagh and Kram 1989).

For running trials two through seven, we played an audible metronome via a custom MATLAB script (Mathworks Inc., Natick, MA, USA) and instructed participants to initiate ground contact simultaneously with the audible metronome sound. An audible metronome has been used in many running studies to alter step time (Cavagna et al. 1991; Farley and González 1996; Hunter and Smith 2007; Morin et al. 2007; Snyder and Farley 2011). The metronome played a sharp, crisp sound at time intervals that matched the respective participant's preferred stride time and at a time interval within the preferred stride time to initiate the contralateral leg's step.

Running trials two and three familiarized participants to running with the metronome and running trials four through seven were used for data analysis. Running trials two and three consisted of running with the most (0%) and least (21%) symmetric step time conditions, respectively. Running trials four through seven were performed with the metronome set at 0, 7, 14, and 21% step time asymmetry in a randomized order (Fig. 1). We chose these step time asymmetry conditions based on pilot testing and previous studies. We found that changing metronome asymmetry < 7% is difficult for a participant to distinguish (e.g., 0 and 4% step time asymmetry sound similar) and a 21% step time asymmetry was chosen as the most asymmetric condition because it is larger than the maximum step time asymmetry observed from 10 athletes with unilateral transtibial amputations



**Fig. 1** Visual depiction of a stride with respective steps denoted for 0, 7, 14, and 21% step time asymmetries. 0% indicates that the first (Step<sub>1</sub>) and second (Step<sub>2</sub>) steps comprising a stride have equal step times. During asymmetric step trials, Step<sub>1</sub> is the “long step” and Step<sub>2</sub> is the “short step”

during running at 2.5 to 3.0 m/s (step frequency asymmetry range: 0 to 16%) (Beck et al. 2017). Moreover, we calculated the absolute value of the symmetry index, expressed as a percentage (*SI*), to establish the magnitude of inter-leg step time ( $t_{\text{step}}$ ) asymmetry.

$$SI = \left| \frac{t_{\text{step},1} - t_{\text{step},2}}{0.5(t_{\text{step},1} + t_{\text{step},2})} \right| \times 100. \quad (1)$$

The metronome always matched the respective participant's preferred stride time, calculated from the respective session's initial running trial.

## Data collection and analyses

We recorded the vertical and anterior–posterior components of the GRFs (1000 Hz) for thirty seconds during the last minute of the initial running trial and during minutes 3 and 5 of running trials 4–7. Next, we filtered GRFs using a fourth-order low-pass Butterworth filter with a 30 Hz cutoff and used the filtered data to calculate spatio-temporal parameters (step time and ground contact time), GRF parameters (peak and stance average vertical GRFs, and peak braking and propulsive GRFs), leg stiffness (as per Farley et al. 1993), as well as the negative and positive external mechanical work over each step (Cavagna 1975) with a custom MATLAB script. We then calculated each biomechanical variable's inter-leg asymmetry using the absolute value of the symmetry index (Eq. 1). We used a vertical GRF threshold of 10 N to establish ground contact.

All participants were instructed to fast for at least three hours prior to testing. We measured rates of oxygen uptake ( $\dot{V}O_2$ ) and carbon dioxide expiration ( $\dot{V}CO_2$ ) using open-circuit spirometry (ParvoMedics TrueOne 2400, Sandy, UT, USA) and averaged these rates over the last two minutes of each trial. We monitored the respiratory exchange ratio (RER) during each trial to ensure that participants were primarily relying on aerobic metabolism, indicated by an RER < 1.0. We used the average  $\dot{V}O_2$  and  $\dot{V}CO_2$  to calculate metabolic power (W) using a standard equation (Brockway 1987). Next, we subtracted the corresponding session's standing metabolic power from each running trial and divided by participant mass (including clothing and shoes) to yield mass-normalized net metabolic power (W/kg).

To relate net metabolic power to the corresponding step time asymmetry, we ensured that participants ran with consistent step times throughout the trial. We did this by implementing a “step time steady-state.” We defined step time steady-state as the percentage difference in step time asymmetry, as per the SI, during minutes 3 and 5 of the symmetric metronome trials. Based on the notion that unimpaired individuals achieve step time steady-state when running to

a symmetric metronome (Cavagna et al. 1991; Farley and González 1996; Hunter and Smith 2007; Morin et al. 2007; Snyder and Farley 2011), we determined that asymmetric running trials achieved a biomechanical steady-state if the step time asymmetry between minutes 3 and 5 was within two standard deviations of the average step time asymmetry from all participants running to the symmetric metronome (Fig. 2).

### Statistical analyses

The only asymmetry trials that we included for statistics were those that achieved a step time steady-state and we only used the data collected over the final minute from those trials. We performed independent linear mixed models to test the influence of step time, ground contact time, peak and stance average vertical GRF, peak braking and propulsive GRF, leg stiffness, and negative and positive external mechanical work asymmetry on the percent change in net metabolic power. Further, we performed independent linear mixed models to assess the influence of step time asymmetry on ground contact time, peak and stance average vertical GRF, peak braking and propulsive GRF, leg stiffness, and negative and positive external mechanical work asymmetry and average values from both legs. For each statistical test, we controlled for the order of experimental session by including session number as a variable in each of our linear mixed models. We report the fixed effect ( $\beta$ ), but not the intercept, for each statistically significant linear mixed model

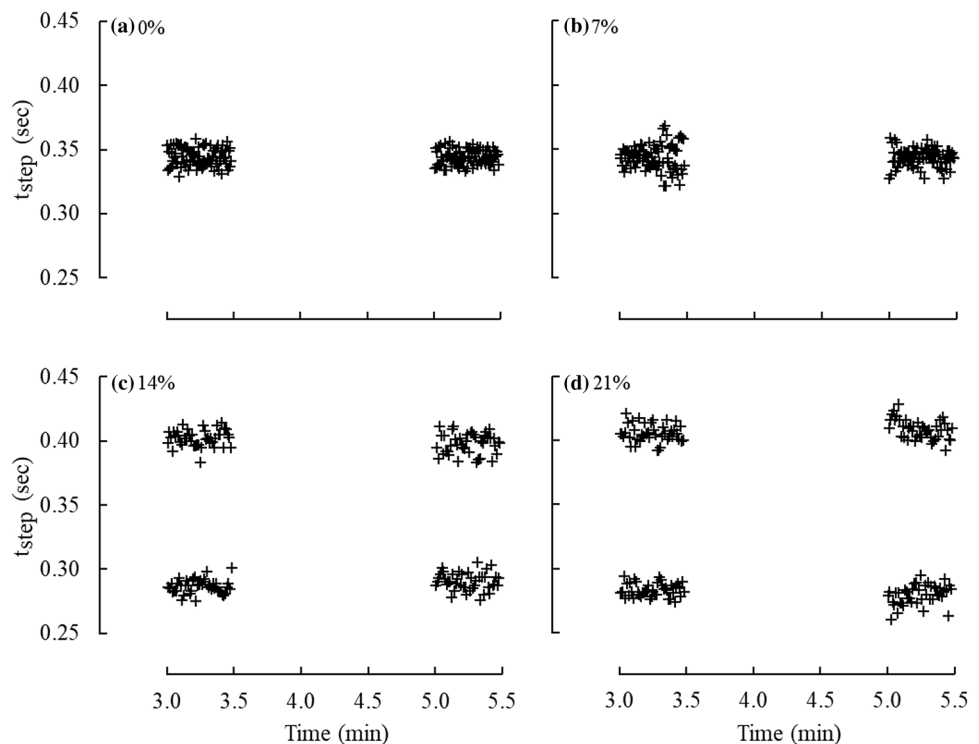
(dependent variable =  $\beta$  independent variable + intercept), because  $\beta$  characterizes the independent variable's influence on the dependent variable. We set significance as  $\alpha = 0.05$  and performed statistical analyses using RStudio software (RStudio, Inc., Boston, MA, USA).

### Results

The step time steady-state was  $0.82 \pm 0.63\%$  (average  $\pm$  SD), thus we only present results using asymmetry trials where the step time SI at minute 5 was  $\leq 2.08\%$  different from minute 3 (Fig. 2). Overall, our participants performed 32 asymmetric running trials (out of 60) that achieved a step time steady-state (session 1: 16 trials from 7 participants, and session 2: 16 trials from 10 participants). Numerically, participants exhibited stride times that were on average  $< 1\%$  different when running with the asymmetric versus symmetric metronome trials. During the symmetric metronome trial, participants exhibited an average step time asymmetry of  $1.7 \pm 0.1\%$  ( $\pm$  SD) (Table 1). Furthermore, the session number did not influence any of the relationships between biomechanical asymmetries and net metabolic power ( $p \geq 0.423$ ), and thus we removed “session” as a fixed effect in our linear mixed model for interpreting our results.

Eight of the nine investigated biomechanical asymmetries affected net metabolic power during running. For every 10% increase in step time asymmetry, net metabolic power increased 3.5% ( $\beta = 0.35$ ;  $p < 0.001$ ) (Fig. 3). For every 10%

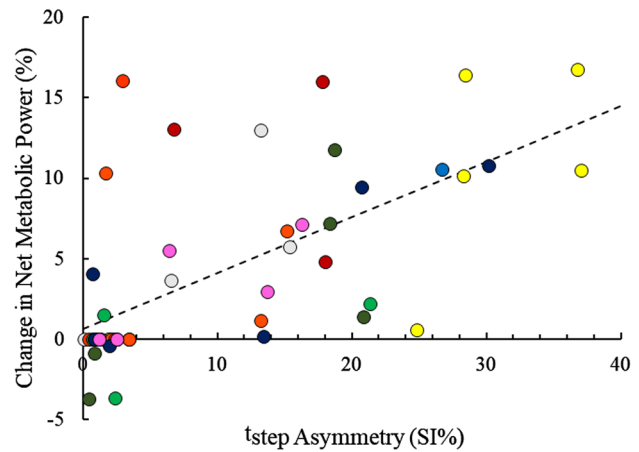
**Fig. 2** Individual step times ( $t_{\text{step}}$ ) for a participant over minutes 3 and 5. The participant ran with a metronome at a symmetry index of, **a** 0%, **b** 7%, **c** 14%, and **d** 21%. For this participant,  $t_{\text{step}}$  steady-state was achieved (less than a 2.08% SI difference between minutes 3 and 5) during trials **a** and **b**, but not **c** or **d**



**Table 1** Average ( $\pm$ SD) biomechanical variables across different step time asymmetry clusters for the leg that took shorter step times (fast) and the leg that took longer step times (slow) during each trial

$t_{step}$ asym (Abs SI%)	$t_{step}$ asymmetry clusters										
	Cluster 1 (1.6 $\pm$ 0.9)		Cluster 2 (6.6 $\pm$ 0.2)		Cluster 3 (15.2 $\pm$ 1.9)		Cluster 4 (20.8 $\pm$ 2.3)		Cluster 5 (31.3 $\pm$ 4.5)		
	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	Fast	Slow	
$t_{step}$ (s)	0.36 $\pm$ 0.02	0.37 $\pm$ 0.02	0.37 $\pm$ 0.02	0.40 $\pm$ 0.02	0.40 $\pm$ 0.02	0.34 $\pm$ 0.02	0.40 $\pm$ 0.02	0.33 $\pm$ 0.02	0.41 $\pm$ 0.03	0.30 $\pm$ 0.01	0.41 $\pm$ 0.01
$t_c$ (s)	0.24 $\pm$ 0.02	0.25 $\pm$ 0.02	0.27 $\pm$ 0.01	0.26 $\pm$ 0.01	0.24 $\pm$ 0.02	0.24 $\pm$ 0.02	0.24 $\pm$ 0.01	0.25 $\pm$ 0.02	0.24 $\pm$ 0.02	0.25 $\pm$ 0.01	0.26 $\pm$ 0.02
Stance Avg vGRF (BW)	1.53 $\pm$ 0.13	1.52 $\pm$ 0.12	1.40 $\pm$ 0.097	1.56 $\pm$ 0.11	1.41 $\pm$ 0.09	1.41 $\pm$ 0.11	1.69 $\pm$ 0.11	1.36 $\pm$ 0.12	1.70 $\pm$ 0.16	1.20 $\pm$ 0.10	1.60 $\pm$ 0.17
Peak vGRF (BW)	2.55 $\pm$ 0.24	2.50 $\pm$ 0.23	2.47 $\pm$ 0.21	2.58 $\pm$ 0.18	2.56 $\pm$ 0.12	2.56 $\pm$ 0.15	2.64 $\pm$ 0.15	2.39 $\pm$ 0.28	2.50 $\pm$ 0.26	2.11 $\pm$ 0.21	2.18 $\pm$ 0.23
Peak braking GRF (BW)	-0.30 $\pm$ 0.03	-0.31 $\pm$ 0.03	-0.29 $\pm$ 0.05	-0.32 $\pm$ 0.05	-0.25 $\pm$ 0.05	-0.25 $\pm$ 0.05	-0.34 $\pm$ 0.05	-0.23 $\pm$ 0.03	-0.35 $\pm$ 0.03	-0.23 $\pm$ 0.04	-0.34 $\pm$ 0.03
Peak propulsive GRF (BW)	0.25 $\pm$ 0.02	0.25 $\pm$ 0.03	0.25 $\pm$ 0.05	0.23 $\pm$ 0.02	0.29 $\pm$ 0.03	0.29 $\pm$ 0.03	0.22 $\pm$ 0.01	0.29 $\pm$ 0.05	0.20 $\pm$ 0.02	0.28 $\pm$ 0.04	0.18 $\pm$ 0.01
$k_{leg}$ (kN/m)	12.1 $\pm$ 1.7	11.6 $\pm$ 1.7	10.9 $\pm$ 1.7	11.8 $\pm$ 1.6	12.7 $\pm$ 2.0	13.1 $\pm$ 1.3	11.3 $\pm$ 1.8	11.3 $\pm$ 1.8	11.7 $\pm$ 1.5	10.4 $\pm$ 0.7	9.8 $\pm$ 1.0
- Ext. Mech Work (J/kg)	1.65 $\pm$ 0.23	1.69 $\pm$ 0.24	1.79 $\pm$ 0.27	1.63 $\pm$ 0.13	2.13 $\pm$ 0.43	1.19 $\pm$ 0.28	2.34 $\pm$ 0.41	2.34 $\pm$ 0.41	1.31 $\pm$ 0.15	2.56 $\pm$ 0.32	0.83 $\pm$ 0.14
+ Ext. Mech Work (J/kg)	1.65 $\pm$ 0.23	1.68 $\pm$ 0.20	1.51 $\pm$ 0.06	1.90 $\pm$ 0.31	1.35 $\pm$ 0.26	1.99 $\pm$ 0.28	1.41 $\pm$ 0.20	1.41 $\pm$ 0.20	2.24 $\pm$ 0.43	1.09 $\pm$ 0.16	2.29 $\pm$ 0.23

We clustered each trial based on its step time asymmetry; Greater clusters indicate more asymmetric step time asymmetry

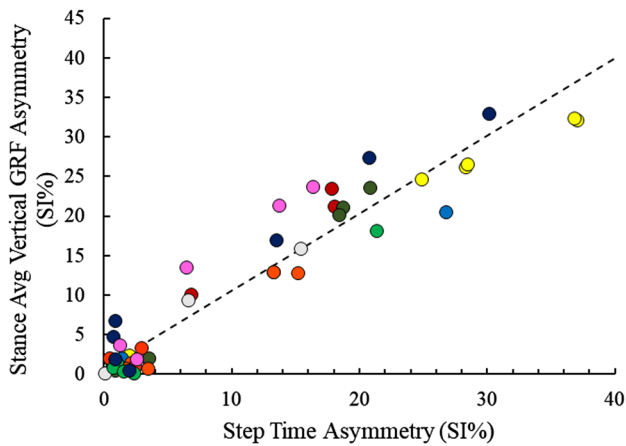


**Fig. 3** Percent change in net metabolic power versus step time asymmetry ( $t_{step}$ ). SI% equals the absolute values of the symmetry index expressed as a percentage. Each color represents a different participant. Dashed line depicts the linear mixed model’s equation: Percent change in net metabolic power = 0.35  $t_{step}$  SI + 0.67 ( $p < 0.001$ )

increase in ground contact time asymmetry, net metabolic power increased 7.8% ( $\beta = 0.78$ ;  $p = 0.036$ ). For every 10% increase in stance average vertical ( $\beta = 0.35$ ;  $p < 0.001$ ), peak braking ( $\beta = 0.13$ ;  $p < 0.001$ ), and peak propulsive GRF ( $\beta = 0.20$ ;  $p < 0.001$ ) asymmetry, net metabolic power increased by 3.5, 1.3, and 2.0%, respectively. Additionally, for every 10% increase in leg stiffness asymmetry, net metabolic power increased 3.9% ( $\beta = 0.39$ ;  $p = 0.042$ ). For every 10% increase in negative ( $\beta = 0.09$ ;  $p < 0.001$ ) and positive ( $\beta = 0.11$ ;  $p < 0.001$ ) external mechanical work, net metabolic power increased 0.9 and 1.1%, respectively. Peak vertical GRF asymmetry did not affect net metabolic power ( $p = 0.469$ ).

Moreover, every 10% increase in step time asymmetry elicited 9.8% more asymmetric stance average vertical GRFs ( $\beta = 0.98$ ;  $p < 0.001$ ) (Fig. 4), 15.1% more asymmetric peak braking GRFs ( $\beta = 1.51$ ;  $p < 0.001$ ), and 11.9% more asymmetric peak propulsive GRFs ( $\beta = 1.19$ ;  $p < 0.001$ ) (Fig. 5; Table 1). Also, every 10% increase in step time asymmetry elicited 28.6% ( $\beta = 2.87$ ;  $p < 0.001$ ) and 20.0% ( $\beta = 2.00$ ;  $p < 0.001$ ) more asymmetric negative and positive external mechanical work values (Table 1). In contrast, step time asymmetry did not affect ground contact time ( $p = 0.189$ ) or leg stiffness ( $p = 0.179$ ) asymmetry. Experimental session order did not influence any of the relationships between step time asymmetry and other biomechanical asymmetries ( $p \geq 0.189$ ) and was removed from these analyses. Step time asymmetry did not affect ground contact time, GRF parameters, or leg stiffness when averaged across both legs ( $p \geq 0.059$ ). Further, step time asymmetry did not affect negative ( $p = 0.399$ ) or positive ( $p = 0.291$ ) external mechanical work averaged across both legs.





**Fig. 4** Stance average (Avg) vertical ground reaction force (GRF) asymmetry versus step time ( $t_{\text{step}}$ ) asymmetry. SI% is the absolute value of the symmetry index expressed as a percentage. Dashed line indicates the relationship between  $t_{\text{step}}$  asymmetry and stance average vertical GRF asymmetry: Stance Avg Vertical GRF Asymmetry =  $0.98 t_{\text{step}}$  asymmetry +  $0.72$ ,  $p < 0.001$

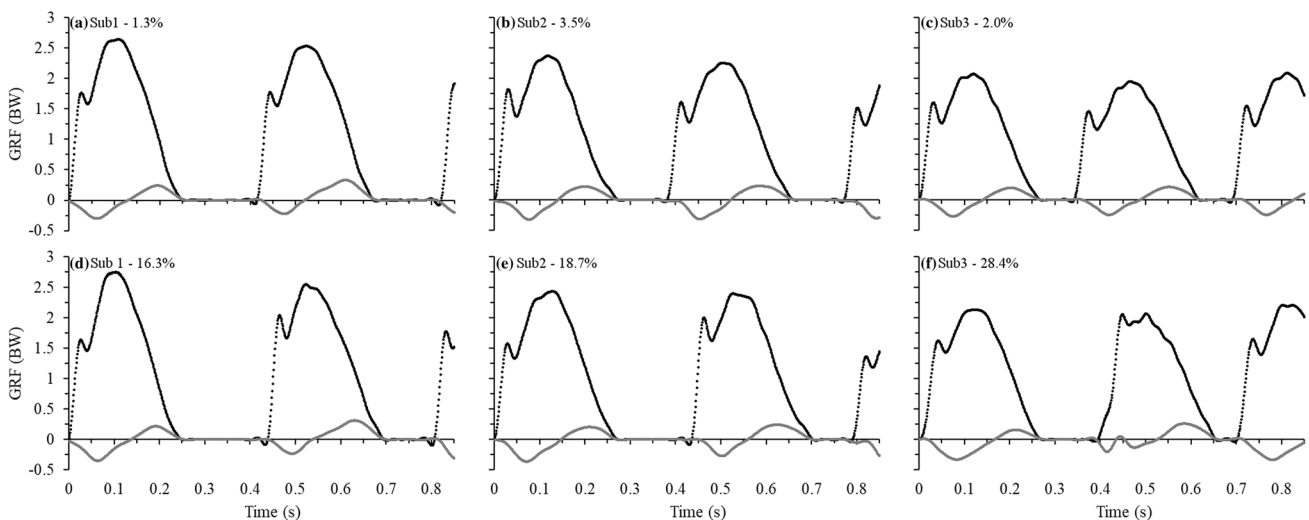
## Discussion

The purpose of this study was to determine how step time asymmetry influences net metabolic power in unimpaired individuals during running. We found that increased step time asymmetry increases net metabolic power during running. Hence, we accept our hypothesis. Unimpaired individuals likely attain better distance-running performance using symmetric versus asymmetric step times due to their lower rates of metabolic energy expenditure (Fuller et al. 2016; Hoogkamer et al. 2016; Joyner 1991). Our

results are in line with a previous study that measured the influence of step time asymmetry on net metabolic power during walking in unimpaired individuals (Ellis et al. 2013). Namely, Ellis et al. (2013) reported that 21–26 and 42% asymmetric step times (as per the symmetry index, Eq. 1) increased net metabolic power during walking by 21–29 and 80%, respectively. Thus, asymmetric step times increase net metabolic power during both walking and running, albeit to a greater extent during walking.

During running, participants achieved asymmetric step times by modulating their ground force production (Fig. 4). To elicit more asymmetric step times, our participants maintained (symmetric) ground contact times and exhibited asymmetric stance average vertical GRFs to produce different aerial times between the legs (Weyand et al. 2010, 2000). Peak and stance average vertical GRFs are usually directly related during running (Munro et al. 1987), however, while running with asymmetric step times our participants exhibited peak and stance average vertical GRF asymmetries that were independent of each other (linear mixed model:  $p = 0.836$ ).

This study's participants may have expended more metabolic energy when running with asymmetric versus symmetric step times because their muscles performed more positive external mechanical work over the respective strides. On level ground, runners perform 0 net external mechanical work (Cavagna and Kaneko 1977; Cavagna et al. 1964; Snyder and Farley 2011). Throughout each running step, elastic mechanisms (e.g., tendons, ligaments, shoe soles) store and release mechanical energy (Alexander 1991; Biewener and Roberts 2000), thereby reducing muscle mechanical work input to sustain running. While muscles need to generate force during running (Kram



**Fig. 5** Vertical (black) and horizontal (gray) ground reaction force (GRF) traces for three participants running with relatively symmetric (a–c) and asymmetric (d–f) step time asymmetries. Each trial's step time asymmetry is indicated in the top left-hand corner of each panel

2000), elastic mechanisms allow muscles to produce force more economically (Ortega et al. 2015) by mitigating gross mechanical work (Biewener and Roberts 2000; Cavagna and Kaneko 1977). During running with asymmetric step times, participants yield net negative external mechanical work over the faster/shorter steps and net positive external mechanical work over the slower/longer steps (Table 1). Specifically, at an average step time asymmetry of 31.3% (SD: 4.5%), participants performed 210% more external mechanical work over the slower/longer step versus the faster/shorter step (Table 1). Since elastic structures cannot generate mechanical work *de novo*, muscles need to input the majority of the slower/longer step's external positive mechanical work. Thus, using increasingly asymmetric step times may elicit less mechanical energy conservation via elastic mechanisms than using symmetric step times, thereby requiring muscles to perform more positive mechanical work per stride. We postulate that the conservation of mechanical energy via elastic leg mechanisms declines as step time asymmetry increases, resulting in more positive muscle mechanical work input over a stride, and in turn, increased metabolic rates.

This study had potential limitations. During data collection, it appeared that participants matched the beat of the metronome, yet very few trials achieved steady-state asymmetric step times that coincided with the metronome beat. Out of 60 asymmetric running trials, only 9 trials reached a step time steady-state and were within 3% of the metronome's asymmetry. Participants did no better at matching the asymmetric beat during the second session compared to the first session. Thus, the difficulty of modulating step time asymmetry was a potential limitation of this study. Still, our metabolic results are similar regardless of whether we used the step time steady-state trials or all 60 trials. Across all 60 trials, for every 10% increase in step time asymmetry, net metabolic power increased by 4.1% (linear mixed model;  $\beta = 0.41$ ;  $p < 0.001$ ), vs. 3.5% during the step time steady-state trials (Fig. 3). Further, it is uncertain whether the increased metabolic rates during running with versus without a metronome were consistent across asymmetry conditions. Moreover, the results of this study may not be generalizable to individuals with asymmetric physical impairments (e.g., pathology, injury, amputation). If an individual has unequal leg characteristics, such as a severe leg length discrepancy, they may or may not minimize metabolic energy expenditure during running using symmetric step times. Rather, individuals with unilateral physical impairments may select asymmetric running biomechanics to minimize metabolic energy expenditure given their physical characteristics. Therefore, cohort-specific investigations are necessary to determine the effectiveness of rehabilitation strategies aimed to elicit symmetric biomechanics and minimize metabolic energy expenditure during running.

## Conclusions

During running, unimpaired individuals minimize metabolic energy expenditure using symmetric, rather than asymmetric, inter-leg step times. To accomplish asymmetric step times, unimpaired participants maintain ground contact times and vary each leg's aerial times by applying different magnitudes of stance average vertical force on the ground. This technique likely reduces the conservation of mechanical energy via elastic structures during running compared to using more symmetric step times, potentially explaining the metabolic differences between running with symmetric versus asymmetric step times. Regardless of the mechanism(s), we confirm that running with asymmetric step times increases the rate of metabolic energy expenditure in unimpaired individuals. Therefore, unimpaired individuals likely utilize symmetric biomechanics to reduce metabolic energy expenditure and enhance distance-running performance.

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**Author contributions** AG, OB, & EA planned the experiment. OB & EA performed data collection. OB & EA analyzed the data. AG, OB, & EA wrote the manuscript.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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