

RESEARCH ARTICLE

Effects of stride frequency and foot position at landing on braking force, hip torque, impact peak force and the metabolic cost of running in humans

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ABSTRACT

Endurance runners are often advised to use 90 strides min^{-1} , but how optimal is this stride frequency and why? Endurance runners are also often advised to maintain short strides and avoid landing with the feet too far in front of their hips or knees (colloquially termed 'overstriding'), but how do different kinematic strategies for varying stride length at the same stride frequency affect economy and impact peaks? Linear mixed models were used to analyze repeated measures of stride frequency, the anteroposterior position of the foot at landing, \dot{V}_{O_2} , lower extremity kinematics and vertical ground reaction forces in 14 runners who varied substantially in height and body mass and who were asked to run at 75, 80, 85, 90 and 95 strides min^{-1} at 3.0 m s^{-1} . For every increase of 5 strides min^{-1} , maximum hip flexor moments in the sagittal plane increased by 5.8% ($P < 0.0001$), and the position of the foot at landing relative to the hip decreased by 5.9% ($P = 0.003$). Higher magnitudes of posteriorly directed braking forces were associated with increases in foot landing position relative to the hip ($P = 0.0005$) but not the knee ($P = 0.54$); increases in foot landing position relative to the knee were associated with higher magnitudes ($P < 0.0001$) and rates of loading ($P = 0.07$) of the vertical ground reaction force impact peak. Finally, the mean metabolically optimal stride frequency was 84.8 ± 3.6 strides min^{-1} , with 50.4% of the variance explained by the trade-off between minimizing braking forces versus maximum hip flexor moments during swing. The results suggest that runners may benefit from a stride frequency of approximately 85 strides min^{-1} and by landing at the end of swing phase with a relatively vertical tibia.

KEY WORDS: Endurance runners, Stride rate, Stride length, Overstride, Kinematics, Running economy

INTRODUCTION

As speed is the product of stride frequency (SF) and stride length (SL), a wide range of SF and SL combinations are possible for a given speed. However, within the endurance running speed range of humans, many experienced runners use a restricted SF range and alter speed primarily by changing SL, regardless of body mass (M_b) and lower extremity length. Cavanagh and Kram (1989) found that runners at 3.15 m s^{-1} compared with 4.12 m s^{-1} increased SL by 26% but increased SF by only 4% from 83 to 86 strides min^{-1} . Similar results were reported by Weyand et al. (2000), who observed no significant change in SF among a sample of 29 runners as they doubled their speed from 2 to 4 m s^{-1} , and only about a 20%

increase in SF up to 8 m s^{-1} , above which increases in speed were primarily a function of SF rather than SL. According to Daniels (2005), Olympic marathon runners run at an approximately 10% slower pace than 5000 m runners but with nearly identical SFs of 91–93 strides min^{-1} . Further, as elite runners fatigue over long distances, their speed decreases primarily from a reduction in SL rather than SF (Buckalew et al., 1985; Hunter and Smith, 2007). Despite these observations, there is considerable inter-individual variation in preferred SF, and for unknown reasons not all studies have shown such constant SFs over a range of speeds. Tokmakidis et al. (1989) found a 15% increase in SF as speed increased from 3 to 6 m s^{-1} in a sample of nine competitive runners, and Elliott and Blanksby's (1979) analysis of 20 non-competitive joggers found a 19% increase in SF in males and a 27% increase in SF in females over speeds from 2.5 to 5.5 m s^{-1} .

One possible reason that some runners tend to modulate speed primarily by changing SL while using a relatively constant SF in the endurance speed range is to minimize metabolic cost. SF and SL both have curvilinear relationships with mass-specific metabolic cost at a given speed (Högberg, 1952). What causes these curvilinear relationships is unknown, but numerous studies document a close correspondence between a runner's metabolically optimal stride frequency (OSF) and preferred stride frequency (PSF) at a given speed, with OSFs between approximately 85 and 90 strides min^{-1} for a range of speeds below 6 m s^{-1} , independent of M_b and lower extremity length (Cavanagh and Williams, 1982; McMahon et al., 1987; Kaneko et al., 1987; Cavanagh and Kram, 1989; Hunter and Smith, 2007; Snyder and Farley, 2011). As noted by Cavanagh and Kram (1989: 43): 'Though previous studies have suggested that there is a most economical stride length at a given speed, our data suggest that there may be a most economical SF at all speeds used in distance running.' Why OSF tends to range between 85 and 90 strides min^{-1} , however, is still poorly understood, as are the factors that lead to variation in PSF. Although elite runners reportedly prefer 85–90 strides min^{-1} in the endurance speed range, less experienced joggers are more likely to use SFs of 78–85 strides min^{-1} at moderate speeds (Nelson and Gregor, 1976; Elliott and Blanksby, 1979; Petray and Krahenbuhl, 1985). In addition, people who habitually run barefoot or in minimal shoes tend to prefer SFs of approximately 85–90 strides min^{-1} (Squadrone and Gallozzi, 2009; Larson and Katovsky, 2012; Lieberman, 2014; Lieberman et al., 2015), and habitually shod runners are more likely to use higher SFs when barefoot than when shod regardless of speed, M_b or lower extremity length (Divert et al., 2008; Squadrone and Gallozzi, 2009; McCallion et al., 2014).

Another possible reason that some runners prefer a restricted SF range is to minimize injury. Although no prospective studies have tested how variations in SF and SL correlate with injury rates, variations in SF and SL affect kinematic and kinetic variables that

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List of abbreviations

COM	center of mass
COT	cost of transport
dO_H	dimensionless landing position of the foot ('overstride') relative to the hip
dO_K	dimensionless landing position of the foot ('overstride') relative to the knee
dSF	dimensionless stride frequency
GRF	ground reaction force
GRF_V	vertical ground reaction force
LMM	linear mixed model
MHFM	maximum hip flexor moment in the sagittal plane during swing
O_H	landing position of the foot ('overstride') relative to the hip
O_K	landing position of the foot ('overstride') relative to the knee
OSF	optimal stride frequency
PSF	preferred stride frequency
SF	stride frequency
SL	stride length
VLR	vertical loading rate of GRF impact peak

are proposed to influence repetitive running injuries (Schubert et al., 2014). Higher SFs and shorter SLs are associated with lower impact peaks of the vertical ground reaction force (GRF_V), lower tibial accelerations at impact, higher peak GRF_V , lower external sagittal knee moments, and increased external sagittal ankle moments (Farley and González, 1996; Mercer et al., 2003; Stergiou et al., 2003; Derrick et al., 1998; Morin et al., 2007; Seay et al., 2008; Heiderscheit et al., 2011). In addition, higher SFs and shorter SLs have been associated with a more flexed knee at impact, less knee excursion during stance, and less vertical excursion of the center of mass (COM) (Cavanagh and Williams, 1982; Farley and González, 1996; Stergiou et al., 2003; Morin et al., 2007; Heiderscheit et al., 2011).

This study addressed several related questions based on the observation that experienced runners tend to prefer a restricted SF range of 85–90 strides min^{-1} across endurance running speeds. First, if SFs between 85 and 90 strides min^{-1} are energetically less costly, what factors influence this narrow range of OSFs? Second, if experienced runners tend to use a relatively small range of SFs and vary speed primarily through changes in SL, what are the biomechanical and energetic consequences of different ways to shorten or lengthen stride?

Mass–spring mechanics provide one possible explanation for observed inter- and intra-individual variation in OSFs. Running is a bouncing gait in which tendons, ligaments and muscles of the lower extremity store elastic energy during the first half of stance and then recoil during the second half of stance (Alexander, 1984). If OSFs maximize the contribution of elastic energy exchange relative to total work, then muscles can perform less mechanical work and expend less metabolic energy (Cavagna et al., 1997). This model is supported by experiments which found that the lower extremity behaves more like a simple spring at a runner's PSF than at slower and faster stride frequencies (Farley et al., 1991; Farley and González, 1996). However, if mass–spring mechanics determine a single OSF, then elastic energy storage should also be optimal at that frequency. In a test of this hypothesis, Snyder and Farley (2011) took advantage of the need for muscles to do additional work to elevate or lower the body's COM during uphill and downhill running. The mass–spring model predicts that variations in SF will affect metabolic cost less on inclined versus flat surfaces because the possibility of elastic energy storage is reduced on slopes. However, inclines of +3 deg

and –3 deg had no significant effect on OSF in nine experienced male runners, indicating that factors other than elastic energy storage also contribute to OSF.

Additional factors to consider are the biomechanical and energetic trade-offs of producing external work (moving the body COM) and internal work (moving parts of the body relative to the COM). Cavagna et al. (1988) showed that running animals tend to use SFs below the symmetrical bouncing frequency that minimizes external work in order to lower the internal work cost of accelerating and decelerating the limb at higher frequencies. In a subsequent study, Cavagna et al. (1991) proposed that OSF is a function of minimizing the average force that muscles exert per step (greater at lower SFs), and minimizing limb stiffness (greater at higher SFs). A related trade-off, noted by Daley and Usherwood (2010), is that while variations in stride length affect leg stiffness, and hence the cost of locomotion, stiffer legs also cause more deflections of the viscera. They propose that optimal economy is influenced by a compromise between leg excursion angles and therefore SLs that maximize leg stiffness versus minimize the work needed to control visceral displacements.

This study measured the effects on OSF of two key variables related to potential trade-offs between internal and external work: the cost of leg swing and the position of the foot at contact relative to the hip and knee. As described above, one energetic consequence of varying SF is to alter the energy required to accelerate the lower extremity during swing. Numerous studies estimate that leg swing contributes approximately 10–30% of the net cost of running (Myers and Steudel, 1985; Cavagna et al., 1988; Modica and Kram, 2005; Marsh et al., 2004). In a simple test of this hypothesis, Doke et al. (2005) found that increasing the frequency of swinging an isolated leg from 42 to 66 cycles min^{-1} increased metabolic cost by 53%. By extrapolation, a 25% increase in SF from 75 to 95 strides min^{-1} should increase the metabolic cost of running by approximately 23%.

The other variable considered here is how far forward a runner's foot lands relative to other parts of the body at the beginning of

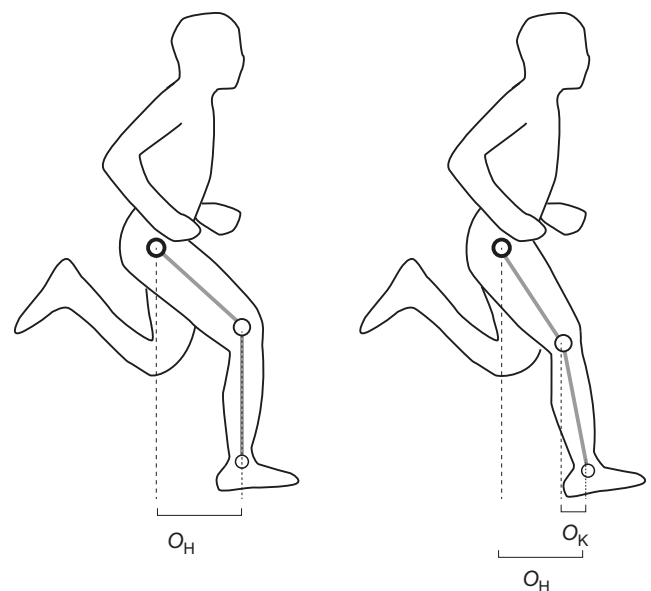


Fig. 1. Kinematic variations in landing position of the foot ('overstride') at foot strike. The left and right figures have the same measure of foot position relative to the hip (O_H) in the sagittal plane, but the right figure has a more anterior position of the foot relative to the knee (O_K) because of less hip flexion and more knee extension at contact.

stance. If endurance runners tend to use a relatively constant SF, then increases in speed must result from a longer SL. However, variations in SL for a given speed can be achieved by a longer aerial phase or from landing with a more protracted lower extremity in which the foot is more anterior to the hip (colloquially known as ‘overstride’). Moreover, there are different kinematic strategies by which a runner can extend SL through protraction of the lower extremity at the end of swing phase. As Fig. 1 shows, a runner’s foot can land in the same position relative to the hip in the sagittal plane (here termed O_H for overstride relative to the hip) either by flexing both the hip and knee more or by flexing the hip less while extending the knee more, with the latter pattern also resulting in the foot landing much further forward relative to the knee (here termed O_K).

In order to consider the effects of these varying kinematic patterns on braking forces, O_H is a critical variable because the further forward the foot lands relative to the COM, the greater the magnitude of the braking impulse that decelerates the body during the first half of stance (Heiderscheit et al., 2011). Therefore, to maintain steady state, the propulsive impulse generated by the body during the second half of stance must increase in proportion to this braking impulse. For practical reasons, we define this distance relative to the hip, O_H , because the hip is close to the human body’s COM, which is also affected by other factors such as trunk lean. Previous studies have not directly measured the effect of variations in O_H on cost, but we predict the effect is likely to be substantial given evidence that anteroposterior forces are approximately four times more costly than vertical forces, and they contribute to more than one-third the cost of running (Chang and Kram, 1999). O_H is also relevant to the collision cost of locomotion because the further forward the foot lands relative to the COM, the greater the distance the foot travels on the ground during stance, increasing the extent to which the COM trajectory must be redirected upward at the end of stance (Lee et al., 2013).

As noted above, because a runner can use different kinematics to change SL, and hence O_H , it is also useful to consider how far forward the foot is relative to the knee in the sagittal plane. In order to make this variable commensurate between forefoot and rearfoot strikers, we define this distance, O_K , as the projected anteroposterior distance of the ankle relative to the knee at the moment of contact. Variations in O_K are likely to have several effects on lower extremity kinematics and kinetics. It is likely that individuals who land with a higher O_K will have a less flexed hip, a more extended knee and a more dorsiflexed ankle, thus

increasing lower extremity stiffness at impact (Hamill et al., 2014). These differences probably have complex effects on cost and the potential for injury. On the one hand, a higher O_K at a given speed may add to the metabolic cost of running by increasing vertical fluctuations of the body’s COM and by increasing eccentric activity by the quadriceps during the first half of stance (Heiderscheit et al., 2011; Lee et al., 2013). On the other hand, a higher O_K may lessen the amount of eccentric activity by the calf muscles during the first half of stance. In terms of injury, if a higher O_K stiffens the leg, it will decrease stability on uneven terrain (Daley and Usherwood, 2010) as well as increase the rate and magnitude of the impact peak, the collisional energy lost during impact, and the rate and magnitude of the GRF_V following impact (Lieberman et al., 2010).

This study tested five hypotheses derived from the model presented above. Hypothesis 1 is that for a given speed, the maximum hip flexor moment necessary to protract the lower extremity during swing is predicted to increase in proportion to SF. Hypothesis 2 is that both O_H and O_K are predicted to vary inversely with SF. Hypothesis 3 is that for a given speed, the impulse caused by braking forces (posteriorly directed forces in the horizontal plane) is predicted to increase in proportion to O_H . A corollary to this hypothesis is that there should be no significant relationship between braking force and O_K after accounting for the effects of O_H . Hypothesis 4 is that increases in O_K will correlate with a more extended lower extremity at impact (as manifested by less hip flexion, more knee extension and more ankle dorsiflexion) and higher rates of loading of the vertical impact peak (VLR) and magnitudes of the GRF_V impact peak. Finally, hypothesis 5 is that although OSF is not expected to be determined entirely by the trade-off between the costs of braking impulse and maximum hip flexor moments in the sagittal plane during swing, a runner’s OSF for a given speed is expected to correlate with the minimum solution for these two costs.

MATERIALS AND METHODS

Subjects

Fourteen individuals (12 males, 2 females) between the ages of 19 and 48 years, sampling a diverse range of heights (1.66–1.97 m, mean 1.84±0.08 m) and M_b (50.2–86.5 kg, mean 72.9±11.6 kg), volunteered for this study (Table 1). All participants were physically fit and experienced runners who ran more than 30 km week⁻¹, and none had any lower extremity injuries that could compromise their gait. All subjects provided informed consent to participate in the experiment, which was approved by the

Table 1. Subject characteristics and observed versus predicted optimal stride frequency

Subject ID	M_b (kg)	Lower extremity length (m)	Measured OSF	Predicted OSF	%Difference
2	71.9	0.94	83.2	83.3	-0.12
3	79.6	0.95	86.1	87.3	-1.29
4	80.1	0.985	84.2	85.0	-0.96
5	75.2	1.01	84.5	84.4	0.22
6	68.7	0.94	86.8	85.2	1.88
7	76	0.98	85.1	85.7	-0.63
8	67.4	0.93	85.9	85.7	0.27
10	85.5	0.99	79.5	80.2	-0.86
11	61.1	0.91	93.4	84.0	11.26
12	50.2	0.81	–	84.2	–
13	50.2	0.92	80.7	84.8	-4.85
14	71.1	0.99	–	86.8	–
15	86.5	0.98	81.4	84.2	0.49
18	87	0.92	86.7	84.3	4.15
Mean±s.d.	72.2±12.0	0.95±0.05	81.4±2.51*	84.7±1.74*	-0.15±4.15*

*Calculated without subject 11 (see Results). Subjects 12 and 14 did not show a curvilinear relationship between stride frequency and cost of transport (COT); therefore, optimal stride frequency (OSF) could not be calculated (see Results). M_b , body mass.

Institutional Review Board of Harvard University. The experiments were conducted at the Skeletal Biology and Biomechanics Lab of the Department of Human Evolutionary Biology at Harvard University.

Treatment

After a warm-up period during which subjects ran for 5 min at 3.0 m s^{-1} at a self-selected SF, each subject was instructed to run at 3.0 m s^{-1} in synchronization with a metronome set to five different SFs. Although some studies measure SF at $\pm 5\%$ and $\pm 10\%$ of preferred SF (e.g. Snyder and Farley, 2011), preferred SFs on a treadmill may not accurately reflect preferred SFs in overground conditions, and it is difficult to run precisely synchronized with a metronome. We therefore asked participants to run as best they could at 75, 80, 85, 90 and 95 strides min^{-1} , and then measured their actual SFs in each trial. Two trials were recorded for each SF once subjects had adjusted their SF to the metronome. First, subjects ran for approximately 30 s on an instrumented treadmill with 3D motion capture to measure aspects of their kinematics and kinetics at each SF trial in random order (details below). Second, subjects were fitted with a nose clip and a respirometry mouthpiece to collect all expired gas. Subjects first stood at rest for 5 min to measure baseline oxygen consumption and become comfortable with the \dot{V}_{O_2} system; subjects then ran for approximately 6–8 min on a standard treadmill (LifeFitness, Rosemont, IL, USA) at each SF in random order (see below).

Kinematics and kinetics

Kinematics and kinetics were measured simultaneously on a treadmill (Bertec, OH, USA) instrumented with two force plates to measure ground reaction forces (GRFs) at 1000 Hz at the same time that 3D motion data were captured at 500 Hz with an 8-infrared camera Oqus motion capture system (Qualysis Corp, Gothenburg, Sweden). Thirteen reflective markers were placed on the following landmarks: the left and right anterior superior iliac spines, the left and right posterior superior iliac spines, the left and right greater trochanters, the medial and lateral epicondyles of the right leg, the medial and lateral malleoli of the right leg, the calcaneus of the right foot, and the second and fifth metatarsal heads of the right foot.

Kinematic and kinetic data were analyzed in Visual 3D (C-Motion, Germantown, MD, USA). Kinematic data were filtered with a 6 Hz low-pass filter, and force-plate data were filtered with a 100 Hz low-pass filter. Segment mass and COM locations of the foot, shank and thigh were calculated in Visual 3D using anthropometric scaling factors provided by Dempster (1955). Each segment was modeled as an elliptical cylinder with length defined as the distance from the distal mediolateral markers to the proximal mediolateral markers defining the segment. The radius of the cylinder at each end was defined as half the distance between the mediolateral markers at the distal and proximal ends of the segment, respectively. The moment of inertia of the segment in each plane was then calculated using the standard formula for a cylinder following Hanavan (1964). Hip, knee and ankle angles were measured on the right limb as the position of the distal segment (thigh, shank and foot, respectively) relative to the proximal limb segment for each joint in the sagittal plane. Angles were calculated at the moment of foot contact with the ground (defined as the first instance of the GRF_V) and at midstance (defined as the point at which anteroposterior forces cross zero from negative to positive). Braking impulses were calculated as the integral of the anteroposterior GRF from foot strike to midstance. Although the cost of swing is the sum of the net mechanical work of accelerating each segment, Doke and Kuo (2007) found that the metabolic cost of swinging the entire lower extremity at different frequencies correlates strongly (Pearson's $r=0.95$) with the peak amplitude of hip flexor moment in the sagittal plane. Consequently, leg swing cost was approximated as the maximum hip flexion moment (MHFM) in the sagittal plane during swing phase. The magnitude of the GRF_V impact transient peak, when present, was identified as the highest force measured during the peak event. Following Lieberman et al. (2010), when a GRF_V transient peak was not present, or was difficult to identify, the magnitude of the GRF_V was measured at 8% of the ground contact time, the average instance of the impact transient occurrence across a group of previously examined subjects. VLR was measured as the slope of the GRF_V force curve between initial ground contact and the peak impact transient event. Five steps in each trial were calculated and averaged for all variables except the impact transient peak and VLR. For these variables, four

steps were averaged except in the case of six subjects who occasionally varied foot strike type within a trial condition altering the occurrence of an impact transient. For these subjects and trials, the most consistent GRF_V profile (i.e. impact transient versus 8% of stance phase) was chosen with a minimum of two steps averaged for analysis.

Respirometry

The energetic cost of running at different SFs was measured using standard open-flow methods (Fedak et al., 1981) in a closed room with constant temperature and humidity. Prior to each experiment, a Sable Systems FlowKit-500H Mass Flow Controller and Pump (Sable Systems International, Las Vegas, NV, USA) was calibrated using a measured flow of N_2 , and then used to pull air continuously at 100 ml min^{-1} through a respirometry mouthpiece attached to a Hans-Rudolf, non-rebreathing T-valve and hose. Subjects also wore a nose clip to prevent non-oral breathing. Subsamples of the expired air were pulled at 100 ml min^{-1} by a gas subsampler (SS-4; Sable Systems International) through a Drierite cobalt chloride desiccant column to remove water vapor. The subsampled air was then pushed at 100 ml min^{-1} into a paramagnetic oxygen analyzer (PA-10 Oxygen Analyzer; Sable Systems International) to measure the fractional amount of O_2 at 100 Hz. The amount of O_2 extracted from the air by the lungs was calculated by subtracting the fraction of expired air that is oxygen from the atmospheric concentration of oxygen (approximately 20.93% O_2). To calculate the rate of O_2 uptake (\dot{V}_{O_2}), the extracted percentage O_2 was corrected for system drift and multiplied by the participant's ventilation rate, measured by the incoming flow rate sensor in the respirometry system as:

$$\dot{V}_{\text{O}_2} = f \left(\left(\text{O}_{2,i} + \frac{(\text{O}_{2,f} - \text{O}_{2,i})T_{\text{ss}}}{T_f - T_i} \right) - \text{O}_{2,\text{ss}} \right), \quad (1)$$

where f is the ventilation flow rate in the mask at steady-state, $\text{O}_{2,i}$ is the initial percentage O_2 measured prior to the trial, $\text{O}_{2,f}$ is the final percentage O_2 at the end of the trial, $\text{O}_{2,\text{ss}}$ is the mean percentage O_2 measured at steady-state, T_{ss} is the time when $\text{O}_{2,\text{ss}}$ was measured, T_i is the time when $\text{O}_{2,i}$ was measured and T_f is the time when $\text{O}_{2,f}$ was measured (Perl et al., 2012; Castillo et al., 2014). Oxygen consumption data were sampled using LabChart over a 5–7 min period until participants reached at least 2 min at a flat, steady-state \dot{V}_{O_2} plateau in which the slope was not significantly different from 0 (Whipp and Wasserman, 1972). $\text{O}_{2,i}$ and $\text{O}_{2,f}$ \dot{V}_{O_2} were normalized for error due to system drift following Perl et al. (2012) by taking a 30 s sample of room air before and after each trial. Net \dot{V}_{O_2} was calculated as gross \dot{V}_{O_2} minus the \dot{V}_{O_2} measured during quiet standing and then converted to mass-specific cost of transport (COT, $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) by dividing \dot{V}_{O_2} by M_b and treadmill speed.

Analysis

In order to compare data between subjects, braking impulse and MHFM in the sagittal plane were normalized to M_b . Because the cost of swing varies in proportion to lower extremity length modeled as a simple pendulum, SF was made dimensionless by dividing it by the leg's natural frequency, following Hof (1996) as:

$$d\text{SF} = \text{SF} / \sqrt{(g/l)}, \quad (2)$$

where g is the gravitational constant on earth and l is standing lower extremity length (measured from the greater trochanter to the floor). Both measurements of anteroposterior foot position relative to the hip and knee were made dimensionless by standardizing to lower extremity length ($d\text{O}_H$ and $d\text{O}_K$).

Because this study used a within-subjects design, linear mixed models (LMMs) were used to test many of the hypotheses. LMMs find the minimum least square regression solution for a continuous dependent variable given several independent predictor variables, with a subject identifier used as the random grouping effect to account for repeated measures on the same individuals. Thus, the mixed model accounts for the effects of subject-specific random variations in an individual's model intercept (McCulloch and Searle, 2001). All variables were first examined for normality using a Shapiro–Wilk test and then standardized as Z-scores. To visualize the bivariate relationship

between variables of interest in the linear models while accounting for other model covariates, partial regression plots were generated by plotting the residuals from two LMM regressions: first, the regression of the response variable (e.g. dO_H , or braking force) against other model covariates (e.g. M_b and leg length) while omitting the independent variable of interest (e.g. dSF or dO_H); and second, the regression of the independent variable of interest (e.g. dO_H , braking force, or peak hip torque) against the remaining model covariates (e.g. M_b and leg length).

Hypothesis 1 – that the cost of leg swing for a given speed increases in proportion to SF – was tested with LMM1 in which MHFM during swing was used as a proxy dependent variable for the cost of swing; dSF and lower extremity length were fixed effects. Hypothesis 2 – that O_H and O_K vary inversely with SF – was tested with LMM2 in which each measure of landing position of the foot was the dependent variable, and with M_b included as a covariate. Hypothesis 3 – that braking forces at a given speed increase in proportion to O_H – was tested by LMM3 in which braking impulse was the dependent variable; dO_H was the fixed effect. The corollary hypothesis, that variations in O_K after correcting for O_H will be independent of braking forces, was also tested using partial regression. Hypothesis 4 – that increases in O_K correlate with less hip flexion, more knee extension and more ankle dorsiflexion at impact, and hence higher rates and magnitudes of the GRF_V impact peak – was tested by using three LMMs: in LMM4a, dO_K was the dependent variable and hip, knee and ankle flexion at impact; in LMM4b, the magnitude of the impact peak was the dependent variable and dO_K was the fixed effect; and in LMM4c, the rate of loading of the impact peak was the dependent variable and dO_K was the fixed effect. Finally, hypothesis 5 – that measured OSF correlates with predicted OSF based on the trade-off between the costs of braking impulse and leg swing – was tested by comparing each subject's measured and predicted OSFs. Measured OSF was calculated from the minima of the best-fit quadratic regression between net COT and measured SF. Predicted OSF was calculated by solving for the intersection of two least square regressions for each subject: measured SF versus braking impulse, and measured SF versus MHFM (with both dependent variables transformed to percentage of maximum values).

All statistics were calculated using JMP Pro statistical software (Version 11.0, SAS Institute, Cary, NC, USA), with statistical significance considered to be a $P < 0.05$. For all mixed effects models, a subject identifier was used as the random grouping effect to account for repeated measures from the same individuals. Models used maximum likelihood estimation to compute model coefficients. Because each variable used in statistical models was transformed to a Z-score, effect sizes for the LMMs are reported and compared below as standardized beta coefficients (β).

RESULTS

All participants (summarized in Table 1) completed all trials with a high correlation ($r = 0.948$, $P < 0.0001$) between each participant's prescribed and measured SF, confirming that all participants were generally able to adjust their SF to the metronome. With the exception of the 95 strides min^{-1} trials, measured SFs differed from prescribed SFs by an average of 0.71 ± 1.4 strides min^{-1} (mean \pm s.d.); for the 95 strides min^{-1} trials, the mean was 92.7 ± 2.5 strides min^{-1} . Accordingly, all data were analyzed using each participant's

measured SF. Four of the participants used mostly forefoot strikes, two used mostly midfoot strikes, and nine used mostly rearfoot strikes. Four of the rearfoot strikers and one midfoot striker switched to forefoot strikes when running at 90 and 95 strides min^{-1} ; one of the forefoot strikers used rearfoot strikes at 75 strides min^{-1} . Table 2 summarizes mean values for key kinematic and kinetic variables measured at each prescribed SF.

In order to test the relationship between SF and MHFM during swing in the sagittal plane, a proxy for the cost of swing (hypothesis 1), Table 3 summarizes the results of LMM1, in which MHFM was the dependent variable, and dSF (see Materials and methods) and lower extremity length were fixed effects. As Table 3 and Fig. 2A illustrate, SF has a strong, significant and positive effect on MHFM after accounting for lower extremity length ($\beta = 0.72$, $P < 0.0001$).

Hypothesis 2 – that dO_H and dO_K vary inversely with SF – is summarized in LMM2 and Fig. 2B. LMM2 shows that, after correcting for M_b as an additional covariate, dSF is negatively associated with dO_H ($\beta = -0.82$, $P = 0.003$; Fig. 2B), but not as strongly associated with dO_K ($\beta = -0.38$, $P = 0.12$). In other words, higher SFs are significantly associated with reduced O_H but not O_K after accounting for covariation between dO_H and dO_K .

LMM3, which tests the third hypothesis – that braking forces at a given speed increase in proportion to SF and O_H – is summarized in Table 3 and Fig. 3. In particular, Fig. 3A shows a strong negative association between braking force and dSF after accounting for M_b ($\beta = -0.591$, $P < 0.0001$). The explanation for this result is the strong positive association ($\beta = 0.89$, $P = 0.0005$) between dO_H and braking impulse after accounting for M_b , summarized in LMM3 of Table 3 and illustrated in Fig. 3B. Further, as our model predicts, Table 3 and Fig. 3C show no significant relationship between braking force and dO_K after controlling for the effects of dO_H ($\beta = -0.14$, $P = 0.54$).

Hypothesis 4 predicts that dO_K at impact correlates inversely with hip flexion, knee extension and ankle dorsiflexion at impact, and that dO_K in turn correlates with higher rates and magnitudes of the GRF_V impact peak. dO_K at impact was positively associated (LMM4a; $P < 0.0001$) with ankle ($\beta = 0.50$), knee ($\beta = 0.83$) and hip angles ($\beta = 0.36$); strongly associated with the magnitude of the impact peak ($\beta = 0.63$, $P < 0.0001$; LMM4b); and less strongly associated with impact peak loading rate ($\beta = 0.18$, $P = 0.07$; LMM4c).

Finally, in terms of the relationship between SF and the net COT, 12 of the 14 subjects (86%) had a curvilinear relationship between SF and COT, with an average R^2 of 0.77 ± 0.16 . In two subjects (subjects 12 and 14), however, the relationship between SF and net COT was linear with no minimum: one with a positive slope ($r^2 = 0.813$), the other with a negative slope ($r^2 = 0.932$). Among the 12 subjects with curvilinear COT results, OSF averaged 84.79 ± 3.62 strides min^{-1} , with a range of 79.5–93.4 strides min^{-1}

Table 2. Mean (± 1 s.d.) kinematic and kinetic variables at each prescribed stride frequency

Variable	SF (strides min^{-1})				
	75	80	85	90	95
SF (strides min^{-1})	75.7 \pm 1.36	80.8 \pm 2.49	84.5 \pm 1.08	89.2 \pm 2.21	92.7 \pm 2.51
COT (ml O_2 kg^{-1} m^{-1})	0.180 \pm 0.05	0.171 \pm 0.04	0.175 \pm 0.05	0.176 \pm 0.05	0.186 \pm 0.05
O_H (m)	0.172 \pm 0.023	0.170 \pm 0.027	0.162 \pm 0.027	0.150 \pm 0.023	0.146 \pm 0.021
O_K (m)	0.009 \pm 0.026	0.008 \pm 0.020	0.002 \pm 0.022	-0.008 \pm 0.016	-0.014 \pm 0.016
MHFM (N m kg^{-1})	0.855 \pm 0.112	0.968 \pm 0.152	1.029 \pm 0.107	1.098 \pm 0.109	1.201 \pm 0.184
Braking impulse (N s kg^{-1})	0.022 \pm 0.003	0.021 \pm 0.003	0.019 \pm 0.002	0.018 \pm 0.002	0.017 \pm 0.002
VLR (BW s^{-1})	65.9 \pm 27.8	59.6 \pm 21.3	52.7 \pm 23.2	49.6 \pm 19.8	50.8 \pm 20.9
Impact peak (BW)	1.51 \pm 0.36	1.49 \pm 0.36	1.33 \pm 0.46	1.16 \pm 0.48	1.09 \pm 0.57

SF, stride frequency; COT, cost of transport; O_H , landing position of the foot ('overstride') relative to the hip; O_K , landing position of the foot ('overstride') relative to the knee; MHFM, maximum hip flexor moment; VLR, vertical loading rate of vertical ground reaction force impact peak; BW, body weight.

Table 3. Linear mixed model (LMM) results

Variable	Coefficient±s.e.	t-value	P-value
LMM1			
dSF	0.723±0.055	13.26	<0.0001
M_b	0.239±0.160	1.49	0.161
LMM2			
dO _H	-0.824±0.260	-3.17	<0.0033
dO _K	-0.383±0.240	-1.59	0.120
M_b	0.386±0.263	1.47	0.179
LMM3			
dO _H	0.891±0.242	3.68	0.0005
dO _K	-0.137±0.221	-0.62	0.537
M_b	-0.402±0.329	-1.22	0.251
LMM4a			
Ankle angle	0.499±0.090	5.61	<0.0001
Knee angle	0.830±0.097	8.60	<0.0001
Hip angle	0.360±0.059	6.09	<0.0001
LMM4b			
dO _K	0.630±0.087	7.25	<0.0001
LMM4c			
dO _K	0.176±0.094	1.87	0.0663

LMM1: association between dimensionless stride frequency (dSF) and maximum hip flexor moment (MHFM) during swing, with MHFM as dependent variable; dimensionless stride frequency (dSF) and body mass (M_b) as fixed effects; and subject as random effect.

LMM2: association between both measures of landing position of the foot (O_H and O_K) and dSF, with dSF as dependent variable; dimensionless landing position of the foot relative to the hip (dO_H), dimensionless landing position of the foot relative to knee (dO_K) and M_b as fixed effects; and subject as random effect.

LMM3: associations between both measures of the landing position of the foot (O_H and O_K) and horizontal braking forces, with horizontal braking force as dependent variable; dO_H, dO_K and M_b as fixed effects; and subject as random effect.

LMM4a: association between hip, knee and ankle angles at foot strike and the landing position of the foot relative to the knee (O_K), with dO_K as dependent variable; hip, knee and ankle angles at foot strike as fixed effects; and subject as random effect.

LMM4b: association between the landing position of the foot relative to the knee (O_K) and impact peak magnitude, with magnitude of vertical GRF impact peak as dependent variable; dO_K as fixed effect; and subject as random effect.

LMM4c: association between the landing position of the foot relative to the knee (O_K) and vertical loading rate (VLR) of impact peak, with VLR of vertical GRF impact peak as dependent variable; dO_K as fixed effect; and subject as random effect.

(Fig. 4A). Measured OSF did not correlate significantly with M_b ($r=0.22$, $P=0.46$), height ($r=0.49$, $P=0.10$), or lower extremity length ($r=0.48$, $P=0.11$).

Differences between the predicted and observed OSFs, summarized in Fig. 4B and Table 1, show that for the 12 individuals in which OSF could be measured, these values differed from predicted OSF based on braking force and hip flexor moments by an average of 0.67 ± 3.4 strides min^{-1} , an average percentage difference of less than 1% ($P=0.871$, Student's *t*-test). These results, moreover, are strongly affected by one outlier, subject 11, whose observed OSF was 4.0 s.d. away from the population mean. When this subject was removed from the analysis following Iglewicz and Hoaglin's (1993) criteria of outlier removal, the average SF difference between expected and observed minimum OSFs was 0.40 ± 1.6 strides min^{-1} . As Fig. 4C shows, the correlation between predicted and observed OSF is moderate and significant ($r=0.71$, $P=0.015$).

DISCUSSION

This study addressed several questions motivated by the evidence that many experienced runners tend to prefer a restricted range of SFs across endurance running speeds. In addition to testing whether SFs of approximately 85 strides min^{-1} are optimal in terms of cost, we tested whether OSFs are influenced by a trade-off between

MHFM during swing, a proxy for the cost of swinging the leg (Doke and Kuo, 2007), which increases with higher SFs, and the cost of braking forces influenced by variations in how far the foot lands in front of the hip or knee (colloquially termed 'overstride'), which increases with longer SLs. We also tested the biomechanical and energetic consequences of different ways to shorten or lengthen stride in order to maintain a given SF at a single speed. Five hypotheses were tested using a within-subjects experimental design in which 14 participants were asked to adopt five different SFs from 75 to 95 strides min^{-1} while running at the same speed.

The first hypothesis, that MHFMs are predicted to increase in proportion to SF for a given speed, was strongly supported by the very high, significant and positive correlation between MHFM and SF after accounting for the effects of M_b and lower extremity length. For the subjects measured in this study, increases of 5 strides min^{-1} increased MHFM by approximately 10.5%, similar to results found by other studies (Cavagna et al., 1997).

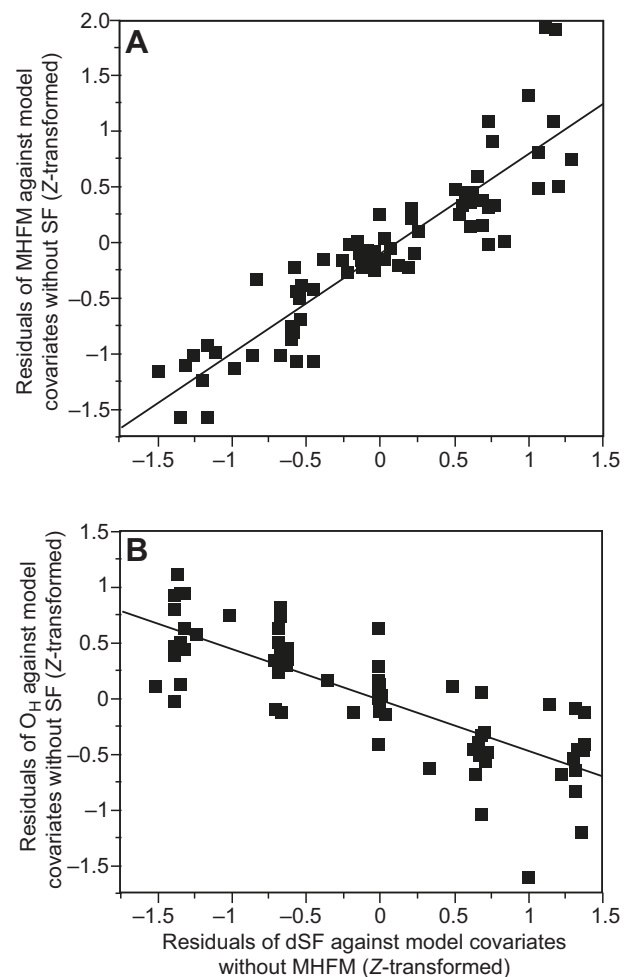


Fig. 2. Partial regressions of dimensionless stride frequency against maximum hip flexor moment during swing and landing position of the foot. In both regressions, the x-axis (independent variable) plots the residuals of the linear mixed model (LMM) of dimensionless stride frequency (dSF) regressed against body mass (M_b , fixed effect) and subject (random effect) without either regression's dependent variable. In A, the y-axis plots the LMM of the residuals of maximum hip flexor moment (MHFM) regressed against M_b and leg length (fixed effects) and subject (random effect) without dSF; in B, the y-axis plots the residuals of LMM of dimensionless landing position of the foot relative to the hip (dO_H) against M_b (fixed effect) and subject (random effect) without dSF. Note that the slopes and *P*-values of the regressions are the same as the coefficients (β) and *P*-values in Table 3.

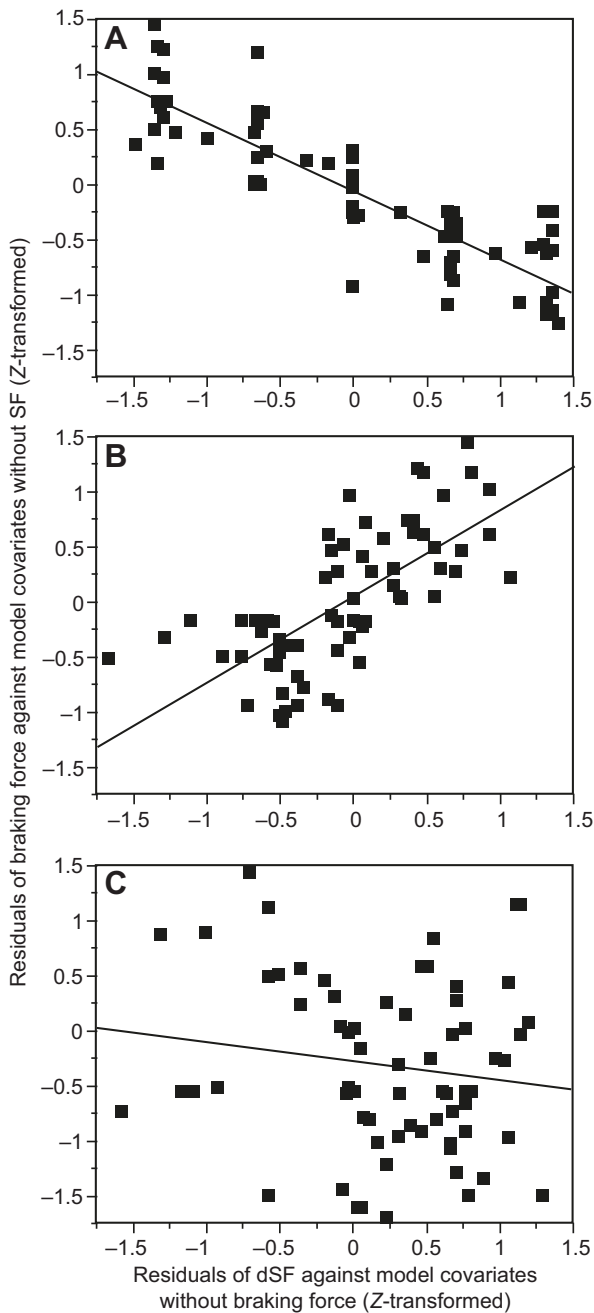


Fig. 3. Partial regressions of braking force against dimensionless measures of foot position at landing ('override') and stride frequency (dSF). In all regressions, the y-axis (dependent variable) plots the residuals of the LMM of horizontal braking force regressed against M_b (fixed effect) and subject (random effect) without the relevant dependent variable. In A, the x-axis plots the residuals of the LMM of dSF regressed against M_b (fixed effect) and subject (random effect) without braking force; in B, the x-axis plots the residuals of LMM of dimensionless landing position of the foot relative to the hip (dO_H) against landing position of the foot relative to the knee (dO_K) and M_b (fixed effects) and subject (random effect) without braking force; in C, the x-axis plots the residuals of LMM of dO_K against dO_H and M_b (fixed effects) and subject (random effect) without braking force. Note that the slopes and P -values of the regressions are the same as the coefficients (β) and P -values in Table 3.

Our results also support the second hypothesis, that both dO_H and dO_K vary inversely with SF. Although higher SFs were significantly and strongly associated with the foot landing closer to the vertical

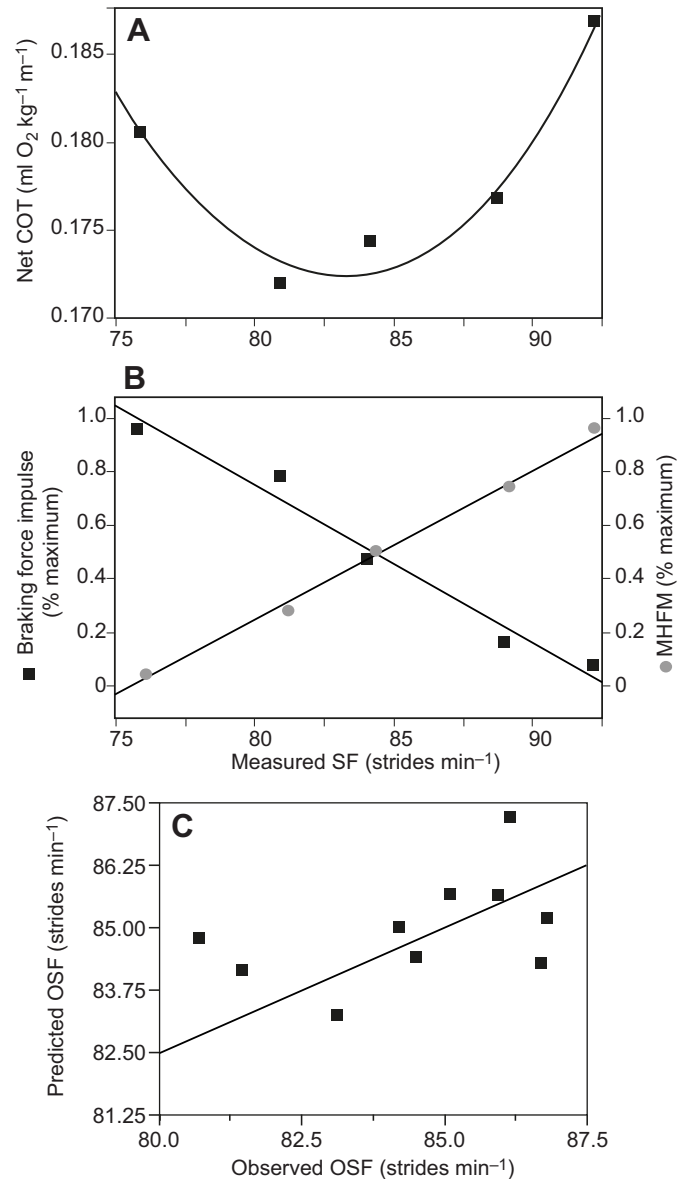


Fig. 4. Variations in stride frequency on cost of transport. (A) Best-fit second-order polynomial regression for average net cost of transport (COT) of the 12 subjects with U-shaped relationships between measured stride frequency (SF) and COT ($r=0.93$, $P=0.02$). (B) Regressions of subject averages for normalized braking impulse against measured SF ($r=0.97$, $P<0.0001$), and normalized MHFM against measured SF ($r=0.98$, $P<0.0001$). (C) Predicted versus observed metabolically optimal stride frequency (OSF) for all subjects (minus one outlier) with U-shaped relationships between SF and COT ($r=0.71$, $P=0.015$).

position of the hip and knee, after accounting for covariation between O_H and O_K , higher SFs were significantly associated with O_H but not O_K . In other words, longer strides at lower SFs were more strongly associated with the foot landing position relative to the hip rather than the knee. This result was corroborated by an additional LMM, which showed that measured SF was most strongly and significantly associated with variations in hip angle at foot strike ($\beta=0.94$, $P<0.0001$), less strongly with knee angle ($\beta=-0.43$, $P=0.07$), and not with ankle angle at foot strike ($\beta=-0.28$, $P=0.21$).

The third hypothesis, that the impulse caused by posteriorly directed braking forces for a given speed increases in proportion to O_H , was also supported. We found strong associations between braking

impulse and dO_H as well as between braking impulse and SF after correcting for M_b (as well as lower extremity length). Thus, as individuals decrease their SF and increase SL by increasing O_H , they substantially alter the trajectory of the COM as predicted by Lee et al. (2013), and they increase the braking impulse that slows the forward movement of the COM in the sagittal plane, corroborating the results of Heiderscheit et al. (2011). In fact, the subjects in this study incurred approximately 6.8% more braking force during the first half of stance for every decrease of 5 strides min^{-1} below optimum. In addition and as predicted, variations in O_K had no significant effect on braking impulse after accounting for the effects of O_H (Fig. 3C). In other words, the braking effects of ‘overstriding’ result from the position of the foot at landing relative to the body’s COM rather than to the position of the foot relative to the knee.

Hypothesis 4, which predicted that increases in O_K would be associated with a more extended lower extremity at impact, leading to higher rates and magnitudes of loading in the GRF_V impact peak, was partially supported. We found that higher O_K was significantly associated with a less flexed hip, a more extended knee and a more dorsiflexed ankle. Although O_K was very significantly associated with the magnitude of the GRF_V impact peak (LMM4b in Table 3), the association between O_K and the rate of vertical loading of the impact peak only approached conventional levels of significance ($P=0.07$; LMM4c in Table 3). These results confirm evidence that other factors which influence lower extremity compliance during impact such as the stiffness of the shoe heel and knee flexion during impact also affect rates of loading (Addison and Lieberman, 2015).

Finally, the results mostly support the fifth hypothesis, that OSF is partly influenced by the trade-off between the costs of braking impulse and leg swing; 86% of the participants showed curvilinear relationships between COT and SF, and their observed OSFs averaged 85 strides min^{-1} . In addition, the predicted OSFs of these individuals based on the intersection of the relationship between SF with braking impulse and MHFM explained about 50% of the variance in measured OSF, with an average difference of only 0.40 strides min^{-1} between predicted and observed OSF (with the exception of one outlier as well as two individuals who lacked an OSF). In fact, the predicted OSFs of 75% of the 12 subjects with curvilinear relationships between COT and SF were within 2 strides min^{-1} of their observed OSFs. Although this study examined only one speed, the results generally support other studies which found that most runners have OSFs of approximately 85 strides min^{-1} independent of M_b and lower extremity length (Högberg, 1952; Petray and Krahenbuhl, 1985; McMahan et al., 1987; Kaneko et al., 1987; Cavanagh and Kram, 1989; Hunter and Smith, 2007; Snyder and Farley, 2011). However, the average OSF measured here was 85 strides min^{-1} , significantly below the 90 strides min^{-1} (one-tailed t -test, $P<0.001$) recommended by some coaches (for review, see Larson and Katovsky, 2012). Further, two of the participants did not have an OSF, and the full range of OSFs was from 79.5 to 93.4, highlighting not only the variability in OSF but also the importance of factors such as lower extremity stiffness not addressed by this study that may also influence OSF.

This study has a number of limitations. First, only one speed was used, yet many of the factors that influence OSF vary in different ways as a function of speed. For example, runners may adjust their kinematics at higher speeds to decrease O_H , and hence braking forces, more effectively for a given SF than they can lessen MHFMs needed to swing the leg. Speed also affects contact time, leg stiffness and other variables that influence elastic energy storage (Farley and González, 1996). A related problem is that runners were

asked to run at a wide range of SFs, some of which were challenging and far from their PSF, perhaps causing participants to alter their kinematics in ways that covary with SF. In addition, this study tested only experienced, fit runners, but the ability to adjust kinematics, and hence cost, may be affected by fitness, experience, strength and other factors that affect internal and external work as well as elastic energy storage. Future studies would benefit from using a wider range of speeds, studying participants with a broader range of experience and skill, and considering additional variables such as limb stiffness, energy lost to collision, as well as variations in trunk lean, strike type and differences in footwear.

Although further research is needed, these results support other findings that most runners likely benefit from a SF of approximately 85 strides min^{-1} . This frequency not only minimizes cost, but also affects kinematics in ways that may be relevant to injury, notably by reducing braking impulses, vertical oscillations of the COM, vertical GRFs and tibial accelerations at impact, and loading at the hip and knee but not the ankle (Farley and González, 1996; Mercer et al., 2003; Stergiou et al., 2003; Derrick et al., 1998; Morin et al., 2007; Seay et al., 2008; Heiderscheit et al., 2011; Chumanov et al., 2012; Lenhart et al., 2014; Schubert et al., 2014).

The other major implication of this study is that, although runners must necessarily increase their SL as they speed up to maintain a constant SF, there appear to be benefits to lengthening one’s stride by increasing O_H without increasing O_K . As Fig. 1 shows, such increases in stride length involve increasing hip flexion rather than knee extension at the end of the swing phase, causing the runner to land with a nearly vertical tibia and with the ankle below the knee. The results of this study indicate that such landings result in lower rates and magnitudes of the impact peak – variables that some studies have implicated in lower rates of several injuries including tibial stress syndrome, Achilles tendonitis, patellofemoral pain syndrome and lower back pain (Milner et al., 2006; Pohl et al., 2009; but see Nigg, 2001). Unless a runner has a very dorsiflexed ankle at foot strike, a more vertical tibia at landing will also cause runners to land with a midfoot or forefoot strike, which has also been observed to be more common among barefoot runners who also typically run with relatively high SFs (Divert et al., 2008; Squadrone and Gallozzi, 2009; Larson and Katovsky, 2012; Lieberman 2012, 2014; McCallion et al., 2014; Lieberman et al., 2015). Such strikes may also lead to lower rates of injuries (Daoud et al., 2012). We conclude there is a need for prospective studies that test the effects of variations in tibial angle at impact and where the foot lands relative to the knee, O_K , on injury.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

D.E.L. and A.G.W. designed the study; J.W. and A.G.W. collected the data; D.E.L., A.G.W. and E.R.C. analyzed the data; D.E.L. wrote the manuscript with help from A.G.W., E.R.C. and J.W.

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References

- Addison, B. J. and Lieberman, D. E. (2015). Tradeoffs between impact loading rate, vertical impulse and effective mass for walkers and heel strike runners wearing footwear of varying stiffness. *J. Biomech.* **48**, 1318–1324.
- Alexander, R. M. (1984). Elastic energy stores in running vertebrates. *Amer. Zool.* **24**, 85–94.

- Buckalew, D. P., Barlow, D. A., Fischer, J. W. and Richards, J. G. (1985). Biomechanical profile of elite women marathoners. *Int. J. Sport Biomech.* **1**, 330-347.
- Castillo, E. R., Lieberman, G. M., McCarthy, L. S. and Lieberman, D. L. (2014). Effects of pole compliance and step frequency on the biomechanics and economy of pole carrying during human walking. *J. Appl. Physiol.* **117**, 507-517.
- 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.
- Cavagna, G. A., Willems, P. A., Franzetti, P. and Detrembleur, C. (1991). The two power limits conditioning step frequency in human running. *J. Physiol.* **437**, 95-108.
- Cavagna, G. A., Mantovani, M., Willems, P. A. and Musch, G. (1997). The resonant step frequency in human running. *Pflügers Arch.* **434**, 678-684.
- Cavanagh, P. R. and Kram, R. (1989). Stride length in distance running: velocity, body dimensions, and added mass effects. *Med. Sci. Sports Exerc.* **21**, 467-479.
- 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.
- Chang, Y. H. and Kram, R. (1999). Metabolic cost of generating horizontal forces during human running. *J. Appl. Physiol.* **86**, 1657-1662.
- Chumanov, E. S., Wille, C. M., Michalski, M. P. and Heiderscheit, B. C. (2012). Changes in muscle activation patterns when running step rate is increased. *Gait Posture* **36**, 231-235.
- Daley, M. A. and Usherwood, J. R. (2010). Two explanations for the compliant running paradox: reduced work of bouncing viscera and increased stability in uneven terrain. *Biol. Lett.* **6**, 418-421.
- Daniels, J. (2005). *Daniels' Running Formula*. Champaign, IL: Human Kinetics.
- Daoud, A. I., Geissler, G. J., Wang, F., Saretsky, J., Daoud, Y. A. and Lieberman, D. E. (2012). Foot strike and injury rates in endurance runners: a retrospective study. *Med. Sci. Sports Exerc.* **44**, 1325-1334.
- Dempster, W. T. (1955). Space requirements of the seated operator: geometrical, kinematic, and mechanical aspects of the body with special reference to the limbs. WADC Technical Report: 55-159, Wright-Patterson Air Force Base.
- Derrick, T. R., Hamill, J. and Caldwell, G. E. (1998). Energy absorption of impacts during running at various stride lengths. *Med. Sci. Sports Exerc.* **30**, 128-135.
- Divert, C., Mornieux, G., Freychat, P., Baly, L., Mayer, F. and Belli, A. (2008). Barefoot-shod running differences: shoe or mass effect. *Int. J. Sports Med.* **29**, 512-518.
- 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.
- Doke, J., Donelan, J. M. and Kuo, A. D. (2005). Mechanics and energetics of swinging the human leg. *J. Exp. Biol.* **208**, 439-445.
- Elliott, B. C. and Blanksby, B. A. (1979). Optimal stride length considerations for male and female recreational runners. *Br. J. Sports Med.* **13**, 15-18.
- Farley, C. T. and González, O. (1996). Leg stiffness and stride frequency in human running. *J. Biomech.* **29**, 181-186.
- Farley, C. T., Blickhan, R., Saito, J. and Taylor, C. R. (1991). Hopping frequency in humans: a test of how springs set stride frequency in bouncing gaits. *J. Appl. Physiol.* **71**, 2127-2132.
- Fedak, M., Rome, L. and Seeherman, H. (1981). One-step N₂-dilution technique for calibrating open-circuit \dot{V}_{O_2} measuring system. *J. Appl. Physiol.* **51**, 772-776.
- Hamill, J., Gruber, A. H. and Derrick, T. R. (2014). Lower extremity joint stiffness characteristics during running with different footfall patterns. *Eur. J. Sport Sci.* **14**, 130-136.
- Hanavan, E. (1964). A mathematical model for the human body. Technical Report, AMRL-TR-64-102: 1-149, Wright-Patterson Air Force Base.
- Heiderscheit, B. C., Chumanov, E. S., Michalski, M. P., Wille, C. M. and Ryan, M. B. (2011). Effects of step rate manipulation on joint mechanics during running. *Med. Sci. Sports Exerc.* **43**, 296-302.
- Hof, A. L. (1996). Scaling gait data to body size. *Gait Posture* **4**, 222-223.
- Högberg, P. (1952). How do stride length and stride frequency influence the energy-output during running? *Arbeitsphysiologie* **14**, 437-441.
- Hunter, I. and Smith, G. A. (2007). Preferred and optimal stride frequency, stiffness and economy: changes with fatigue during a 1-h high-intensity run. *Eur. J. Appl. Physiol.* **100**, 653-661.
- Igiewicz, B. and Hoaglin, D. C. (1993). *How to Detect and Handle Outliers*. Milwaukee, WI: ASQC Quality Press.
- Kaneko, M., Matsumoto, M., Ito, A. and Fuchimoto, T. (1987). Optimum step frequency in constant speed running. In *Biomechanics X-B* (ed. B. Jonsson), pp. 803-807. Champaign, IL: Human Kinetics Publishers.
- Larson, P. M. and Katovsky, W. (2012). *Tread Lightly: Form, Footwear, and the Quest for Injury Free Running*. New York, NY: Sky Publishing.
- Lee, D. V., Comanescu, T. N., Butcher, M. T. and Bertram, J. E. A. (2013). A comparative collision-based analysis of human gait. *Proc. R. Soc. B Biol. Sci.* **280**, 20131779.
- Lenhart, R. L., Thelen, D. G., Wille, C. M., Chumanov, E. S. and Heiderscheit, B. C. (2014). Increasing running step rate reduces patellofemoral joint forces. *Med. Sci. Sports Exerc.* **46**, 557-564.
- Lieberman, D. E. (2012). What we can learn about running from barefoot running: an evolutionary medical perspective. *Exerc. Sport Sci. Rev.* **40**, 63-72.
- Lieberman, D. E. (2014). Strike type variation among Tarahumara Indians in minimal sandals versus conventional running shoes. *J. Sport Health Sci.* **3**, 86-94.
- Lieberman, D. E., Venkadesan, M., Werbel, W. A., Daoud, A. I., D'Andrea, S., Davis, I. S., Mang'eni, R. O. and Pitsiladis, Y. (2010). Foot strike patterns and collision forces in habitually barefoot versus shod runners. *Nature* **463**, 531-535.
- Lieberman, D. E., Castillo, E. R., Otarola-Castillo, E., Sang, M. K., Segei, T. K., Ojiambo, R., Okutoyi, P. and Pitsiladis, Y. (2015). Variation in foot strike patterns among habitually barefoot and shod runners in Kenya. *PLoS ONE* **10**: e0131354.
- 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.
- McCallion, C., Donne, B., Fleming, N. and Blanksby, B. (2014). Acute differences in foot strike and spatiotemporal variables for shod, barefoot or minimalist male runners. *J. Sports Sci. Med.* **13**, 280-286.
- McCulloch, C. E. and Searle, S. R. (2001). *Generalized, Linear, and Mixed Model*. New York, NY: John Wiley.
- McMahon, T. A., Valiant, G. and Frederick, E. C. (1987). Groucho running. *J. Appl. Physiol.* **62**, 2326-2337.
- Mercer, J. A., Devita, P., Derrick, T. R. and Bates, B. T. (2003). Individual effects of stride length and frequency on shock attenuation during running. *Med. Sci. Sports Exerc.* **35**, 307-313.
- Milner, C. E., Ferber, R., Pollard, C. D., Hamill, J. and Davis, I. S. (2006). Biomechanical factors associated with tibial stress fracture in female runners. *Med. Sci. Sports Exerc.* **38**, 323-328.
- Modica, J. R. and Kram, R. (2005). Metabolic energy and muscular activity required for leg swing in running. *J. Appl. Physiol.* **98**, 2126-2131.
- Morin, J. B., Samozino, P., Zameziati, K. and Belli, A. (2007). Effects of altered stride frequency and contact time on leg-spring behavior in human running. *J. Biomech.* **40**, 3341-3348.
- Myers, M. J. and Steudel, K. (1985). Effect of limb mass and its distribution on the energetic cost of running. *J. Exp. Biol.* **116**, 363-373.
- Nelson, R. C. and Gregor, R. J. (1976). Biomechanics of distance running: a longitudinal study. *Res. Q.* **47**, 417-428.
- Nigg, B. M. (2001). The role of impact forces and foot pronation: a new paradigm. *Clin. J. Sport Med.* **11**, 2-9.
- Pert, D. P., Daoud, A. I. and Lieberman, D. E. (2012). Effects of footwear and strike type on running economy. *Med. Sci. Sports Exerc.* **44**, 1335-1343.
- Petray, C. and Krahenbuhl, G. (1985). Running training instruction on running technique, and running economy in 10-year-old males. *Res. Q. Exerc. Sport* **56**, 251-255.
- Pohl, M. B., Hamill, J. and Davis, I. S. (2009). Biomechanical and anatomic factors associated with a history of plantar fasciitis in female runners. *Clin. J. Sport Med.* **19**, 372-376.
- Schubert, A. G., Kempf, J. and Heiderscheit, B. C. (2014). Influence of stride frequency and length on running mechanics: a systematic review. *Sports Health* **6**, 210-217.
- Seay, J., Selbie, W. S. and Hamill, J. (2008). In vivo lumbo-sacral forces and moments during constant speed running at different stride lengths. *J. Sports Sci.* **26**, 1519-1529.
- 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.
- Squadrone, R. and Gallozzi, C. (2009). Biomechanical and physiological comparison of barefoot and two shod conditions in experienced barefoot runners. *J. Sports Med. Phys. Fitness* **49**, 6-13.
- Stergiou, N., Bates, B. T. and Kurz, M. J. (2003). Subtalar and knee joint interaction during running at various stride lengths. *J. Sports Med. Phys. Fitness* **43**, 319-326.
- Tokmakidis, S. P., Léger, L. and Tsarouchas, L. (1989). Energy cost and stride rate variability of elite runners on the treadmill. *Biomech. Sports* **5**, 422-433.
- Weyand, P. G., Sternlight, D. B., Bellizzi, M. J. and Wright, S. (2000). Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J. Appl. Physiol.* **89**, 1991-1999.
- Whipp, B. J. and Wasserman, K. (1972). Oxygen uptake kinetics for various intensities of constant-load work. *J. Appl. Physiol.* **33**, 351-356.