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Effects of independently altering body weight and mass on the energetic cost of a human running model

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ABSTRACT

The mechanisms underlying the metabolic cost of running, and legged locomotion in general, remain to be well understood. Prior experimental studies show that the metabolic cost of human running correlates well with the vertical force generated to support body weight, the mechanical work done, and changes in the effective leg stiffness. Further, previous work shows that the metabolic cost of running decreases with decreasing body weight, increases with increasing body weight and mass, and does not significantly change with changing body mass alone. In the present study, we seek to uncover the basic mechanism underlying this existing experimental data. We find that an actuated spring-mass mechanism representing the effective mechanics of human running provides a mechanistic explanation for the previously reported changes in the metabolic cost of human running if the dimensionless relative leg stiffness (effective stiffness normalized by body weight and leg length) is regulated to be constant. The model presented in this paper provides a mechanical explanation for the changes in metabolic cost due to changing body weight and mass which have been previously measured experimentally and highlights the importance of active leg stiffness regulation during human running.

1. Introduction

Running over level ground requires a significant amount of energy despite the energy storage and return of spring-like legs (Cavagna et al., 1977). There are many components of human running that impart a metabolic cost, including supporting the weight of the body (Farley and McMahon, 1992; Kram and Taylor, 1990; Taylor et al., 1980; Teunissen et al., 2007), braking and propelling the body center of mass in the horizontal direction (Chang and Kram, 1999), swinging the legs about the hip (Gottschall and Kram, 2003; Modica and Kram, 2005; Moed and Kram, 2005), and swinging the arms (Arellano and Kram, 2011; Pontzer et al., 2009).

Prior studies show that generating force to support body weight, or the gravitational force acting on the body, is the primary determinant of the metabolic cost of running (Farley and McMahon, 1992; Kram and Taylor, 1990; Taylor et al., 1980; Teunissen et al., 2007). To better understand the metabolic cost required to support the weight of the body, prior experiments manipulated the effective body weight and mass of runners using weights attached to the waist and a reduced gravity apparatus over an instrumented treadmill (see Fig. 1 for an illustration of previous experiments and Supplemental material for further discussion). These experiments showed that the net metabolic rate of running decreased linearly as body weight was reduced (Farley and McMahon, 1992; Teunissen et al., 2007), increased in direct or slightly more than direct proportion to added body weight and mass (Epstein et al., 1987; Taylor et al., 1980; Teunissen et al., 2007), and was not significantly different from normal running with added mass alone (Teunissen et al., 2007).

The mechanisms that can explain these trends in the metabolic cost of running with changing mass and gravity are not well understood. Prior work shows that the metabolic cost of running is directly proportional to the whole-body mechanical work done by the body over a range of relatively slow running speeds near 3 m/s (Arampatzis et al., 2000; Bijker et al., 2001; Cavagna et al., 1977; Farris and Sawicki, 2012; Ito et al., 1983; Kaneko, 1990; Lacour and Bourdin, 2015). Though the precise relationship between the mechanical work performed by muscle-tendon units in the leg and the metabolic cost of running is complex (Albracht and Arampatzis, 2013; Arampatzis et al., 2006; Farris and Sawicki, 2012; Fletcher et al., 2013, 2010; Lacour and Bourdin, 2015), examining the total mechanical work done at the whole-body level may provide insight into the changes in the metabolic cost of running with changes in mass and gravity.

Further, a recent study showed that the effective stiffness of the leg increases during human running almost in direct proportion to increased body weight (Silder et al., 2015). This almost proportional increase in leg stiffness coincides with a similar increase in the metabolic cost of running with added body weight, indicating that changes in leg stiffness appear to correlate with changes in

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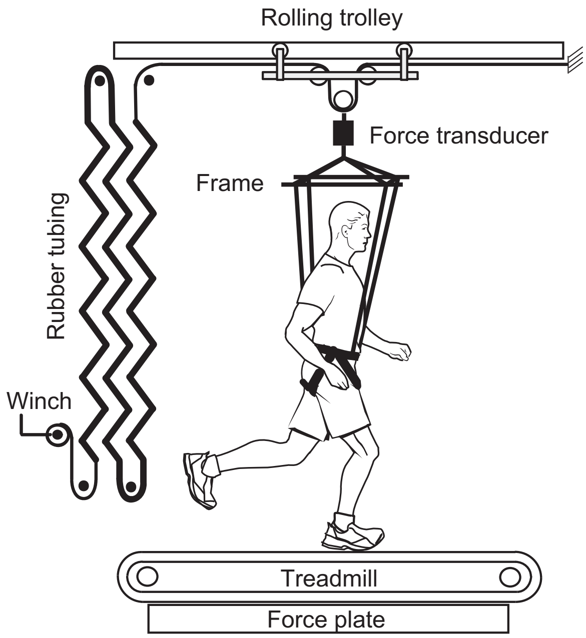

Fig. 1. Reduced gravity apparatus (reproduced/adapted with permission from Teunissen et al. (2007)).

the metabolic cost of running and body weight. Further, since the effective leg stiffness is often approximated by dividing vertical ground reaction force by the effective leg deflection (Silder et al., 2015), we expect that there is a connection between leg stiffness and generating vertical force to support body weight, which is the primary determinant of the metabolic cost of running. Recent modeling work suggests that a strong connection between the chosen leg stiffness and the mechanical cost of transport may exist for humans and animals (Shen and Seipel, 2015a).

We hypothesize that the changes in the metabolic cost of human running with varying body weight and mass (Teunissen et al., 2007) can be largely explained by the changes in the positive mechanical work done (Farris and Sawicki, 2012) during running if a dimensionless relative leg stiffness is maintained (Blickhan and Full, 1993; Shen and Seipel, 2015a). To this end, we developed a relatively simple open-loop mathematical model of human running to calculate the positive mechanical work done during running when body weight and mass were independently varied and leg stiffness was fixed or changed in proportion to body weight and mass. Our results show that changes in the positive mechanical work done by the leg in the simulation closely correlate with the changes in the metabolic cost of human running measured experimentally when the dimensionless relative leg stiffness is maintained. The model provides a mechanistic explanation for the energetic trends of human running and highlights the importance of active leg stiffness regulation during human running.

2. Methods

2.1. Actuated SLIP model of human running

Prior work shows that the whole body center of mass motion during human running can be approximated by a mass bouncing in the sagittal plane on a spring-like leg, like a pogo stick, as represented by the spring-loaded-inverted-pendulum (SLIP) model (Blickhan and Full, 1993; Blickhan, 1989). Since the canonical SLIP model is energy conserving, we required a model which has a mechanism for energy input and removal to study the effects of body weight and mass on the energetic cost of running.

In the present study, we used a variant of the recently developed Hip-Actuated SLIP model of legged locomotion (Shen and Seipel, 2012): See Fig. 2. This model has been shown to be highly-stable across a wide range of parameters and can predict

Table 1
The parameters used to approximate human running in this study were based on prior experimental work and chosen such that the model was stable over the parameter range with fore-aft dynamics that resemble human running. Many of the effective human parameters may change in practice while running based on subject variability, such as the leg stiffness, damping, human body mass, landing angle, and leg torque. We estimated and fixed the model parameters based on the available data for an average human runner.

Parameter	Name	Value
k	Leg stiffness	$k = mg^*K_{rel}/L_0$ N/m (Blickhan and Full, 1993)
K_{rel}	Dimensionless relative leg stiffness	20–25 (Farley and Gonzalez, 1996; Shen and Seipel, 2015a)
c	Effective “bilinear” leg damping	20,000 Ns/m^2 (Abraham et al., 2015)
m	Human body mass	63.3 kg (Teunissen et al., 2007)
l_0	Effective leg length from the human center of mass to the distal leg position (Foot)	1 m (Geyer et al., 2006; Shen and Seipel, 2012)
β	Leg landing angle beta	65° (Shen and Seipel, 2012)
τ	Leg torque	Variable (Table 2)
v_t	Target running speed	3 m/s (Teunissen et al., 2007)
g	Gravity	9.81 m/s^2

realistic center-of-mass dynamics of human running using approximate human parameters. Unlike the traditional energy-conserving SLIP model, the open-loop Hip-Actuated SLIP model inputs energy into the system by torqueing the effective spring-leg about the hip and removes energy from the system through a damper acting along the leg. The parameters used in this model were selected to approximate the average human subject in a prior experiment (Teunissen et al., 2007) for comparison and are summarized in Table 1.

The equations of motion of the Hip-Actuated SLIP model can be derived via Newton's method (Shen and Seipel, 2012). The angle θ of the leg during the stance phase with respect to the horizontal axis is

$$\theta = \frac{\pi}{2} - \tan^{-1}\left(\frac{x - x_f}{y}\right) \tag{1}$$

The “foot” position x_f is the distal point of the effective spring-leg in contact with the ground at leg touchdown during the stance phase, or the approximate foot center of pressure. The position of the body center of mass is described by the coordinates x and y.

The leg length of the effective spring-leg and its derivative during the stance phase are

$$l = \sqrt{\left((x - x_f)^2 + y^2\right)} \tag{2}$$

$$\dot{l} = \frac{(x - f)\dot{x} + y\dot{y}}{l} \tag{3}$$

The forcing along the legs can be described by the force in the effective leg-spring and the effective damping force,

$$F_L = k(l_o - l) - c\dot{l}(l_0 - l) \tag{4}$$

It is important to note that in the present model we used a “bilinear” damping term $(l_0 - l)$ (Abraham et al., 2015) instead of a more typical linear damping term as was used in prior work (Potwar et al., 2014; Shen and Seipel, 2015a, 2015b, 2012). The bilinear damping model was chosen because it enables the Hip-Actuated SLIP model to approximate human ground reaction forces more accurately than the linear damping model (Abraham et al., 2015). The lowest leg damping parameter which ensured stability for all simulations was $c = 14{,}000$ Ns/m^2, but we chose $c = 20{,}000$ Ns/m^2 in this paper based on the value used in prior work which showed a good agreement between the simulated vertical ground reaction forces and experimental data (Abraham et al., 2015). We also show results for varying leg damping and a linear damping model in the supplemental material section.

Initially, we assumed that the leg stiffness k was a constant value despite changing mass and gravity conditions. However, a recent study showed that the effective stiffness of the leg increases almost in direct proportion to added body mass during human running (Silder et al., 2015). Therefore, we hypothesized that the leg stiffness k may vary to maintain a constant dimensionless relative leg stiffness, K_{rel}. Prior work has shown that humans and animals tend to adapt their leg stiffness to maintain an approximately constant dimensionless effective stiffness, which varies between 10 and 20 for animal

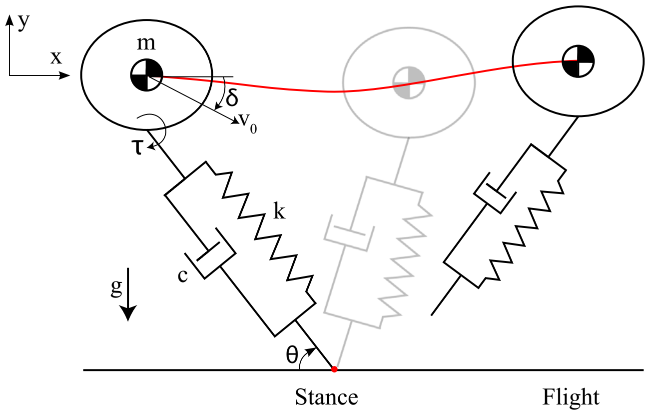

Fig. 2. The Hip Actuated SLIP model of running (Shen and Seipel, 2012).

and human legs (Blickhan and Full, 1993; Shen and Seipel, 2015a).

$$K_{rel} = \frac{k\, l_0}{mg} \tag{5}$$

According to this relationship, the human leg stiffness is related to body mass and gravity, or body weight. The leg stiffness k values for a given K_{rel} are calculated as

$$k = \frac{mgK_{rel}}{l_0} \tag{6}$$

To better understand the effect of leg stiffness, we compared experimental data with (A) a constant leg stiffness k and (B) a constant dimensionless relative stiffness K_{rel} (which changes the leg stiffness k). The resulting parameter values are listed in Table 2 for two representative conditions.

The forcing due to the torque about the hip is

$$F_T = \frac{\tau}{l} \tag{7}$$

In this model, the effective torque about the hip is approximated as a constant value during each stride. In reality, the human leg can generate complex torque and force profiles due to the relative contributions of the ankle, knee, and hip joints and changes in the mechanics of gait (Winter, 2009). Although existing stable and tractable models of legged locomotion do not include anatomical-level detail of the leg, and the constant hip torque model used by the existing actuated SLIP model is a highly-simplified and reduced representation of human running, we found that the model is nonetheless able to approximate the overall whole body dynamics, forces, and energetics of human running.

In the present model, changing parameters such as the effective body mass and weight while keeping other parameters constant changes the average steady state running speed. To maintain the same average running speed of 3 m/s as used in prior work (Teunissen et al., 2007), the constant leg torque τ was discretely adjusted from stride to stride (Table 2) using a numerical solver to maintain a constant 3 m/s average running speed during each running cycle, defined here as one touchdown to the next touchdown.

During running, the model has a distinct stance phase where the effective leg-spring is in contact with the ground and a flight phase where the leg leaves the ground and the body undergoes projectile motion. The equations of motion during the stance phase of running with one leg in contact with the ground are

$$\ddot{x} = \frac{F_T \sin\theta - F_L \cos\theta}{m}, \tag{8}$$

$$\ddot{y} = \frac{F_L \sin\theta + F_T \cos\theta}{m} - g. \tag{9}$$

The model starts in the stance phase when the leg just touches the ground at a given touchdown angle $\theta = \beta$, which occurs when

$$y = l_0 \sin\beta \tag{10}$$

The initial velocity conditions of the model starting from a touchdown event are v_0 and δ, which represent the magnitude and angle of the touchdown velocity vector of the body mass.

The torque τ rotates the leg while the leg is compressed during the stance phase, storing energy in the effective leg spring in preparation for lifting off the ground. When the vertical forces in the spring and damper along the leg become zero, the system achieves the lift off condition and enters the flight phase. The lift off condition is

$$F_L \sin\theta + F_T \cos\theta = 0 \tag{11}$$

The equations of motion during the flight phase of running are

$$\ddot{x} = 0 \tag{12}$$

$$\ddot{y} = \frac{F_S}{m} - g \tag{13}$$

The model transitions back to the stance phase when the next leg touches the ground again at the touchdown angle $\theta = \beta$.

Over one stride at steady-state, the positive mechanical work done is zero because the positive and negative mechanical work cancel. Prior experimental work shows that the total positive mechanical work done by the ankle, knee, and hip joints is directly related to the metabolic cost of running (Farris and Sawicki, 2012). Negative work done was not considered because the efficiency of negative work is significantly higher than positive work and likely adds negligible systemic error since the total positive and negative work done is equal (Farris and Sawicki, 2012).

Here we take a similar approach by calculating the positive mechanical work done to compare with the metabolic cost of running measured experimentally. The large majority of the positive mechanical work done in the model is due to the active leg torque input. The effective leg spring also does some positive work when the energy stored in the leg spring at the beginning of stance is released in the second half of stance, but here we focus on the non-conservative active energy input from the leg torque (see supplemental material for further discussion). The leg damping does purely negative work.

The instantaneous power P_τ of the active torque input during the stance phase is calculated by multiplying the torque and the angular leg velocity,

$$P_\tau = \tau\dot{\theta} \tag{14}$$

Table 2
The conditions used in the simulation match those used experimentally in prior work (Teunissen et al., 2007), where BM = body mass, BW = body weight, m = effective body mass, m_0 = nominal body mass = 63.3 kg, g = effective gravity, and g_0 = nominal gravity = 9.81 m/s^2. The resulting leg stiffness k and constant leg torque τ values used in the model are shown for two representative cases with (A) a constant leg stiffness k and (B) a constant dimensionless relative leg stiffness K_{rel}. The % positive mechanical work from the simulation is shown for direct comparison with the experimental data.

%BM/%BW	Mass and gravity parameter	k = 10–15 KN/m			K_{rel} = 20–25			Experimental data (Teunissen et al., 2007)
		Leg stiffness k (KN/m)	Torque τ (Nm)	% Positive mechanical work	Leg stiffness k (KN/m)	Torque τ (Nm)	% Positive mechanical work	% Metabolic cost
100/100	$\boldsymbol{m = m_0\ g = g_0}$	**10–15**	**215–274**	**100**	**12.4–15.5**	**243–281**	**100**	**100**
100/75	$m = m_0\ g = 0.75g_0$	10–15	267–323	95.0–94.6	9.3–11.6	259–286	82.0–80.6	81 ± 1.7
100/50	$m = m_0\ g = 0.5g_0$	10–15	293–354	89.5–89.3	6.2–7.8	247–266	65.5–62.8	62 ± 2.1
100/25	$m = m_0\ g = 0.25g_0$	10–15	309–372	84.4–84.5	3.1–3.9	223–233	51.0–47.2	45 ± 2.7
110/110	$m = 1.1m_0\ g = g_0$	10–15	209–272	101.9–103.4	13.7–17.1	253–303	108.6–110	114 ± 2.7
120/120	$m = 1.2m_0\ g = g_0$	10–15	202–267	102.7–105.8	14.9–18.6	265–324	117.2–119.9	124 ± 3.2
130/130	$m = 1.3m_0\ g = g_0$	10–15	194–260	102.5–107.2	16.1–20.2	279–348	125.8–130	138 ± 3.8
110/100	$m = 1.1m_0\ g = g_0/1.1$	10–15	234–292	101–101.7	12.4–15.5	261–300	101.3–101.9	105 ± 1.9
120/100	$m = 1.2m_0\ g = g_0/1.2$	10–15	245–306	101.7–103	12.4–15.5	274–313	102.4–103.4	103 ± 1.7
130/100	$m = 1.3m_0\ g = g_0/1.3$	10–15	251–315	102.2–104.3	12.4–15.5	282–321	103.2–104.6	104 ± 3.0

$$\dot{\theta} = \frac{(x_f - x)\dot{y} + y\dot{x}}{x^2 - 2x_f x + x_f^2 + y^2}. \tag{15}$$

The positive mechanical work W_τ done by the active torque input is calculated from the integral of the instantaneous power over time

$$W_\tau = \int P_\tau dt \tag{16}$$

During the flight phase, the body mass undergoes projectile motion, so mechanical work is only done by the leg torque during the stance phase. In reality, there is a metabolic cost associated with leg swing (Gottschall and Kram, 2003; Modica and Kram, 2005; Moed and Kram, 2005), but it is a relatively small contribution to the overall metabolic cost of running.

3. Results

3.1. Reduced weight

If the human leg stiffness k is constant as the effective body weight is reduced, the % change in the positive mechanical work done in the simulation decreases at a much smaller rate than the % change in the metabolic cost of running measured experimentally (Teunissen et al., 2007) (Fig. 3A). The relationship between the positive mechanical work and the percentage normal body weight is similar when the leg stiffness k is varied from 10,000 to 15,000 N/m.

If K_{rel} is maintained as the effective body weight is reduced, the % change in the positive mechanical work done in the simulation decreases and closely correlates with the % change in metabolic cost of running measured experimentally (Teunissen et al., 2007) (Fig. 3B). Increasing K_{rel} from 20 to 25 slightly improves the agreement between the simulation and the experimental results.

3.2. Increased weight and mass

When the leg stiffness k is constant while the body weight and mass increases, the % change in the positive mechanical work performed in the simulation slightly increases, but at a significantly smaller rate than the % change in the metabolic cost of running measured experimentally (Teunissen et al., 2007) (Fig. 4A). The relationship between the positive mechanical work and the percentage normal body weight is similar when the leg stiffness k is varied from 10,000 to 15,000 N/m, but the slope slightly increases.

When K_{rel} is maintained while the body weight and mass increases, the % change in the positive mechanical work performed in the human running simulation increases at a smaller rate than the % change in metabolic cost measured experimentally (Teunissen et al., 2007) (Fig. 4B). Increasing K_{rel} from 20 to 25 improves the agreement between the simulation and the experimental results.

3.3. Increased mass alone

When the leg stiffness k remains constant while the effective body mass alone is increased, the % change in the positive mechanical work done in the human running simulation slightly increases, matching the % change in the metabolic cost of running measured experimentally (Teunissen et al., 2007) (Fig. 5A). The relationship between positive mechanical work and % body mass does not significantly change when the leg stiffness k varies from 10,000 to 15,000 N/m.

Similar results are obtained when K_{rel} is maintained while the effective body mass alone increases (Fig. 5B). Since K_{rel} is assumed to be proportional to the product of mass and gravity, the effective leg stiffness k remains constant when mass is increased and gravity is decreased in proportion. Therefore, the results are similar to those obtained with the constant leg stiffness assumption. Increasing K_{rel} from 20 to 25 also does not significantly change the agreement between the simulation and experimental results.

4. Discussion

The mechanism of spring-mass running with a constant dimensionless relative leg stiffness K_{rel} and varying body mass and weight can predict changes in positive mechanical work done that match changes in the metabolic cost of human running measured experimentally. The model shows that the metabolic trends of human running can be largely explained by a dynamic actuated spring-mass model of running where the effective leg stiffness is regulated to maintain a constant relative leg stiffness.

4.1. Leg stiffness regulation

The model results highlight the importance of active leg stiffness regulation during running. When the body weight is reduced, the model predictions do not closely correlate with experimental data if the leg stiffness k is constant. When the dimensionless leg stiffness K_{rel} is regulated to be constant while the body weight is reduced, the leg stiffness k is reduced in proportion to the effective gravity g (Eq. (6)), and the change in positive mechanical work done in simulation correlates with the change in metabolic cost during running. A similar phenomenon occurs when body weight and mass are increased, except that the leg stiffness is increased in proportion to the increased body mass m for a constant K_{rel} (Eq. (6)).

When body mass alone is increased, both the constant leg stiffness k and dimensionless leg stiffness K_{rel} produce a nearly identical prediction which approximately matches the experimental metabolic cost data. Increasing body mass alone requires one to increase the body mass m and simultaneously reduce the effective gravity g in direct proportion so the overall effective body weight mg is constant. Therefore, K_{rel} and k will be similar with increased mass alone (Eq. (6)) and result in very similar predictions for this special case of system manipulation.

Since the effective leg stiffness is often approximated by dividing the peak vertical ground reaction force by the effective leg deflection (Silder et al., 2015), we expect that there is a connection between leg stiffness and generating vertical force to support body weight, which is the primary determinant of the metabolic cost of running (Farley and McMahon, 1992; Kram and Taylor, 1990; Taylor et al., 1980; Teunissen et al., 2007). Recent modeling work suggests a strong connection between the chosen leg stiffness and the mechanical cost of transport for humans and animals (Shen and Seipel, 2015a).

The effective stiffness of the human leg increases during running almost in direct proportion to added body weight (Silder et al., 2015). This almost proportional increase in leg stiffness coincides with a similar increase in the metabolic cost of running with added body weight, indicating that changes in leg stiffness correlate with changes in the metabolic cost of running and body weight. Our results provide further evidence that leg stiffness should increase with increased body weight and that there exists a relationship between leg stiffness and the metabolic cost of running.

Prior work shows that leg stiffness is roughly constant with decreasing body weight (He et al., 1991). However, analysis of this published data shows that the leg stiffness decreased by approximately 25% on average when body weight was reduced from 100% to 20%. Despite the uncertainty and relatively low subject number available for this existing data set ($n=4$), our model provides support that leg stiffness likely is reduced on average as body weight is reduced during running. However, the model overestimates the reduction in leg stiffness observed due to the assumed linear relationship between leg stiffness and gravity in the definition of K_{rel} (Eq. (6)). The human body may have physiological limitations on the range of leg stiffnesses it can achieve. Though we expect that leg stiffness k decreases on average as human body weight is reduced, the precise change in stiffness may be more complex than the simple linear relationship between k and K_{rel} used in the model.

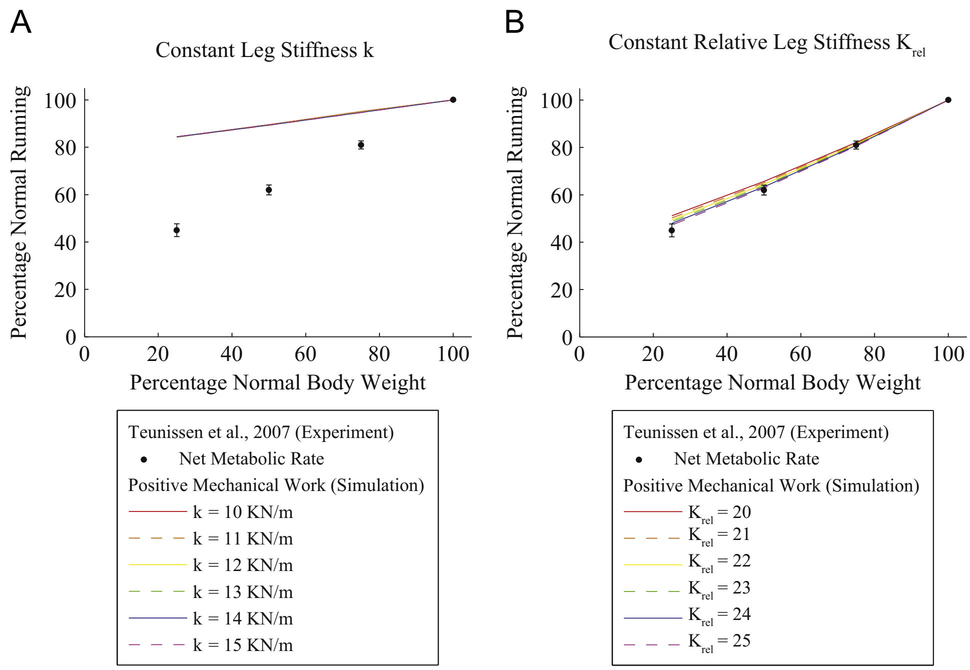

Fig. 3. (A) When the leg stiffness k remains constant while the effective body weight is reduced, the % change in the positive mechanical work performed in the human running simulation decreases but does not correlate well with the % change in the metabolic cost of running measured experimentally (Teunissen et al., 2007). The relationship between positive mechanical work and % body weight is very similar for different k values between 10 and 15 KN/m. (B) When the dimensionless relative leg stiffness K_{rel} is maintained as the effective body weight decreases, the % change in the positive mechanical work from the human running simulation closely correlates with the % change in the metabolic cost measured experimentally (Teunissen et al., 2007). Increasing K_{rel} from 20 to 25 slightly improve the agreement between the simulation and experimental results.

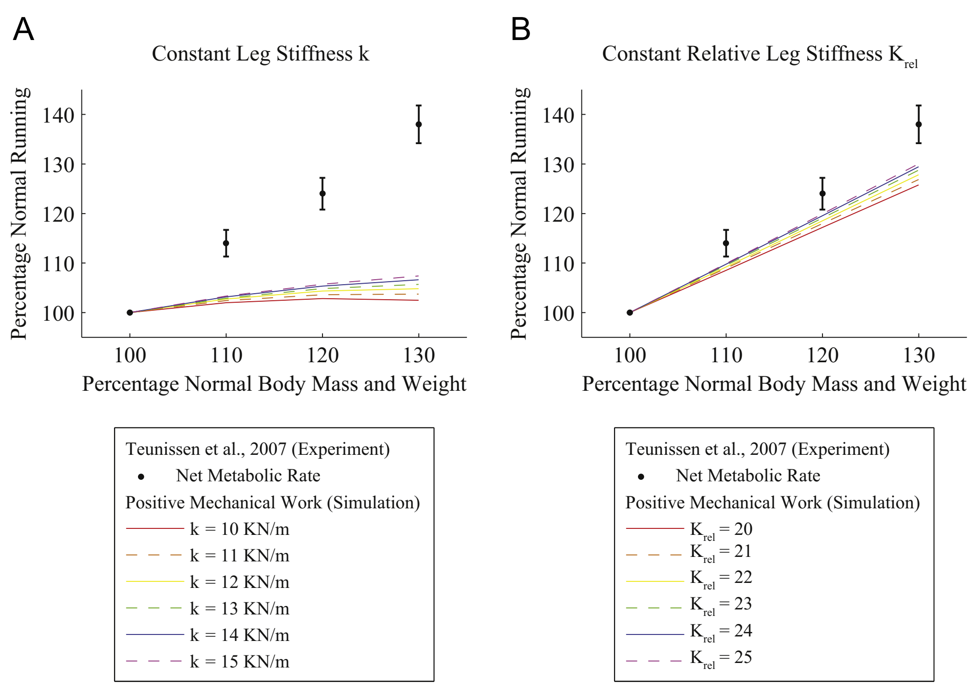

Fig. 4. (A) When the leg stiffness k remains constant while the body mass and weight is increased, the % change in the positive mechanical work performed in the human running simulation does not match the % change in the metabolic cost of running measured experimentally (Teunissen et al., 2007). The relationship between the positive mechanical work and % body mass and weight is similar when the constant leg stiffness is changed from 10 to 15 KN/m, but the slope slightly increases and begins to approach the experimental data. (B) When the dimensionless relative leg stiffness K_{rel} is maintained as the effective body mass and weight increases, the % change in the positive mechanical work from the human running simulation correlates well with the % change in metabolic cost measured experimentally (Teunissen et al., 2007). Increasing K_{rel} from 20 to 25 improves the agreement between the simulation and experimental results.

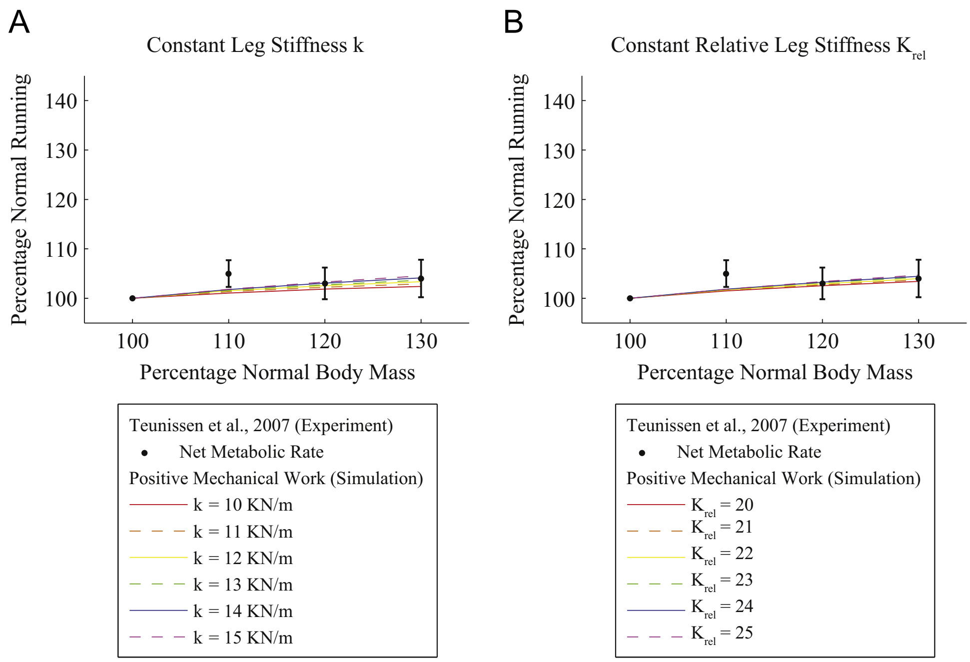

Fig. 5. (A) When the leg stiffness k remains constant while the effective body mass alone is increased (Table 2), the % change in the positive mechanical work performed in the human running simulation closely matches the % change in the metabolic cost of running measured experimentally (Teunissen et al., 2007). The relationship between positive mechanical work and % body mass is similar when the leg stiffness changes from 10 to 15 KN/m. (B) When the dimensionless relative leg stiffness K_{rel} is maintained as the effective body mass alone increases, the % change in the positive mechanical work done in the human running simulation slightly increases along with the experimental metabolic data. The results are very similar to those obtained with a constant leg stiffness k (A). Increasing K_{rel} from 20 to 25 does not significantly change the trend.

No prior experimental data on leg stiffness with increased mass alone exists for comparison with the simulation results. However, prior work shows that the peak vertical ground reaction forces are not significantly different with increased mass alone compared with normal running (Teunissen et al., 2007). Further, the contact time per step, aerial time per step, and duty factor did not significantly change with added mass alone compared to normal running, so it is unlikely that significant changes in leg deflection occurred. If the peak vertical ground reaction force and leg deflection did not significantly change with increase mass alone, then the leg stiffness would not significantly change, which also correlates with the metabolic cost results.

4.2. Relationship between energetic cost and body weight

By extrapolating the reduced gravity results to 0% body weight, the simulation predicts that supporting body weight accounts for approximately 66–71% of the positive mechanical work performed during running (assuming K_{rel}=20–25). This result matches the prior experimental estimate which showed that supporting the weight of the body comprises approximately 73.8 $\pm$ 6.1% of the metabolic cost of running (Teunissen et al., 2007). Since this model does not include swinging legs or arms, the remaining 29–34% of the positive mechanical work may be required propel the body horizontally. Chang and Kram (Chang and Kram, 1999) found that braking/propelling the body horizontally constitutes approximately 39% of the metabolic cost of running at 3.3 m/s, which is near the model prediction. In reality, supporting body weight and braking/propelling the body mass horizontally are not wholly independent tasks, but these estimates based on the simulated change in positive mechanical work provide further insight into the relative contribution of each task to the energetic cost running.

When body weight and mass increase, the model predicts that the positive mechanical work increases in slightly less than direct proportion. The metabolic cost measured experimentally by Teunissen et al. (2007) increased in slightly more than direct proportion to body weight and mass. Other researchers found that increasing body weight and mass is directly proportional to the metabolic cost of running (Epstein et al., 1987; Taylor et al., 1980). While the precise relationship between increasing body weight and mass and the metabolic cost of running varies slightly in the literature, a linear direct relationship appears to be a good approximation.

4.3. Effect of different torque and leg damping models

We also experimented with different leg torque and damping models in addition to the constant torque and bilinear leg damping model presented here (see Supplemental material). Despite relatively large changes in the torque and leg damping models, we still observed similar overall changes in the positive mechanical work, indicating that the fundamental changes in the energetic cost during running are relatively insensitive to the specific leg torque or damping model used.

5. Conclusion

This work demonstrates the importance of leg stiffness regulation during locomotion, even with large changes in body mass and gravity. It shows that a simple mathematical model can predict changes in the experimental metabolic cost of human running if a dimensionless relative leg stiffness is maintained. Also, this work shows that it may be possible for the total positive mechanical work done in a mathematical model to be directly related to the metabolic cost of human running.

One limitation of the simple whole-body model is that it does not make direct predictions about the role of particular muscle groups or joint moments. However, the simple whole-body model provides a framework for the overall effect of joint moments and muscles which can enable future work to determine the specific role of joint moments and particular muscle groups.

Due to its predictive power, the model presented here can provide a foundation for predicting how the metabolic cost of human running is affected by large parameter changes, load carriage, ground terrain properties, and related studies of interest.

Conflict of interest statement

The authors have no conflicts of interest to report in this paper.

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Appendix A. Supplementary material

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