

RESEARCH ARTICLE

What determines the metabolic cost of human running across a wide range of velocities?

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ABSTRACT

The ‘cost of generating force’ hypothesis proposes that the metabolic rate during running is determined by the rate of muscle force development ($1/t_c$, where t_c =contact time) and the volume of active leg muscle. A previous study assumed a constant recruited muscle volume and reported that the rate of force development alone explained ~70% of the increase in metabolic rate for human runners across a moderate velocity range (2–4 m s⁻¹). We hypothesized that over a wider range of velocities, the effective mechanical advantage (EMA) of the lower limb joints would overall decrease, necessitating a greater volume of active muscle recruitment. Ten high-caliber male human runners ran on a force-measuring treadmill at 8, 10, 12, 14, 16 and 18 km h⁻¹ while we analyzed their expired air to determine metabolic rates. We measured ground reaction forces and joint kinematics to calculate contact time and estimate active muscle volume. From 8 to 18 km h⁻¹, metabolic rate increased 131% from 9.28 to 21.44 W kg⁻¹. t_c decreased from 0.280 s to 0.190 s, and thus the rate of force development ($1/t_c$) increased by 48%. Ankle EMA decreased by 19.7±11%, knee EMA increased by 11.1±26.9% and hip EMA decreased by 60.8±11.8%. Estimated active muscle volume per leg increased 52.8% from 1663±152 cm³ to 2550±169 cm³. Overall, 98% of the increase in metabolic rate across the velocity range was explained by just two factors: the rate of generating force and the volume of active leg muscle.

KEY WORDS: Energetics, Locomotion, Running economy, Biomechanics

INTRODUCTION

Zuntz (1897) was the first to quantify the metabolic cost of running in dogs, horses and humans. He noted that each species showed an increasing linear relationship between metabolic rate (in W kg⁻¹) and velocity. In the ensuing years, nearly all terrestrial vertebrates studied have also exhibited a linear relationship between metabolic rate and running velocity. Additionally, previous studies have found that running is metabolically more expensive for smaller compared with larger animals per kg body mass (Taylor et al., 1970, 1982; Heglund et al., 1982).

To explain the size-dependent metabolic cost of running, Taylor et al. (1980) proposed the ‘cost of generating force’ hypothesis. They found that when running animals carried extra weight, their rates of oxygen consumption (\dot{V}_{O_2}) increased in almost direct

proportion to the total weight supported. The vertical force exerted on the ground averaged over an entire stride period increased proportionally with the load but generating one newton of force on the ground was much more costly for smaller animals, such as mice and rats, than for larger animals, such as horses. Taylor (1985) reasoned that this was because, compared with larger animals, smaller animals (e.g. a mouse) must take quicker strides using faster, less economical muscle fibers.

A decade later, Kram and Taylor (1990) refined the cost of generating force hypothesis to also explain why metabolic rate increases at faster running velocities. At any running velocity, the vertical force exerted on the ground by all the feet, averaged over a complete stride, remains the same and is equal to the animal’s body weight. However, the time of individual foot–ground contact, t_c (i.e. the time when force can be applied to the ground) decreases at faster running velocities. Knowing that the rate of force development reflects the intrinsic shortening velocity of muscle (Stevens and Renaud, 1985), Kram and Taylor (1990) reasoned that $1/t_c$ reflects the rate of muscle force generation during each contact phase and hence the rate of cross-bridge cycling. Formally, they hypothesized that the rate of metabolic energy consumption (\dot{E}_{met}) in watts per newton of body weight (W_b) would be equal to the inverse of t_c multiplied by a cost coefficient (c) (Eqn 1). Indeed, across wide velocity ranges of running, bipedal hopping, as well as quadrupedal trotting and galloping, the cost coefficient changed little for a diverse assortment of mammals ranging widely in body size (0.12–200 kg), indicating that metabolic rate was inversely proportional to t_c .

$$\frac{\dot{E}_{\text{met}}}{W_b} = c \cdot \frac{1}{t_c} \quad (1)$$

Eqn 1 is simple because, based on Biewener (1989), Kram and Taylor (1990) assumed that in a given animal, generating a newton of force on the ground requires the same active muscle volume at all running velocities. Subsequently, Roberts et al. (1998) confirmed that the energetic cost of running in humans and bipedal birds could also be explained by the cost of generating force hypothesis, as quantified in Eqn 1.

Pontzer and colleagues have since developed alternative derivations of the cost of generating force hypothesis. Initially, Pontzer (2005) proposed and tested a model (LiMb) for the metabolic cost of running that included a cost for swinging the limbs (assumed to be zero by Kram and Taylor, 1990) and it also fractionated the cost of generating force on the ground into vertical and horizontal force components. Kram and Taylor (1990) assumed that vertical force dominated. Most relevant to the present study, Pontzer (2005) collected data for nine humans running at velocities ranging from 1.75 to 3.5 m s⁻¹. Although the LiMb model does not use direct measurements of contact time, it essentially uses the same $1/t_c$ approach as Kram and Taylor (1990) to estimate the cost of generating force on the ground. The LiMb model estimates limb

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List of symbols and abbreviations

A	cross-sectional area
c	traditional cost coefficient
EMA	effective mechanical advantage
\dot{E}_{\max}	maximum rate of metabolic energy consumption
\dot{E}_{met}	rate of metabolic energy consumption
F_m	net muscle force
GRF	ground reaction force
k	cost coefficient
L	fascicle length
$M_{\text{net joint}}$	joint moment
r	muscle–tendon moment arm
R	GRF moment arm
RER	respiratory exchange ratio
t_c	ground contact time
$1/t_c$	rate of muscle force development
v	velocity
V_m	active muscle volume
\dot{V}_{CO_2}	rate of carbon dioxide production
\dot{V}_{O_2}	rate of oxygen consumption
W_b	body weight

swing costs based on the force required to accelerate the limbs and Pontzer (2005) determined a cost parameter that best fitted the data. Pontzer (2005) concluded that for human running, taking into account limb swing costs explained more of the variance ($R^2=0.43$) in their data than using $1/t_c$ alone ($R^2=0.29$). However, Pontzer (2007) reported that the LiMb model could account for 75% of the variance ($R^2=0.75$) in metabolic rate across running velocity in a different group of human runners but did not offer a definitive explanation for the inconsistency.

Recently, Pontzer (2016) proposed a modified version of the LiMb model: the activation–relaxation and cross-bridge cycling model or ARC model. He argued that the metabolic cost of activation–relaxation of muscle rather than cross-bridge cycling dominates the metabolic cost of generating force during level running. However, the fundamental equation in the ARC model remains numerically equivalent to the original Kram and Taylor (1990) formulation (Eqn 1), in that the metabolic rate is proportional to active muscle volume and $1/t_c$. As Pontzer (2016) notes, additional *in situ* and/or *in vitro* experiments on isolated muscle are needed to determine the relative contributions of activation–relaxation and cross-bridge cycling ATP costs during muscle actions that replicate those of *in vivo* muscles during locomotion.

The volume of leg extensor muscle activated (V_m) is critical to the Kram and Taylor (1990) and Pontzer (2016) formulations of the cost of generating force approaches. V_m is determined by the architecture of the limbs/muscles, and the muscle forces required to support body weight, and decelerate and accelerate the body's center of mass. The muscle forces needed are determined by how the limbs act as a series of levers. Each of the leg segments (thigh, shank and foot) acts as a lever with a fulcrum at the respective joint center. Over the stance phase, changes in limb posture affect the ground reaction force (GRF) moment arm, R (defined as the perpendicular distance from the resultant GRF vector to the respective joint center). The lever arm (perpendicular distance) of the muscle force vector relative to the joint center defines the internal muscle–tendon moment arm (r). The effective mechanical advantage (EMA) is the ratio of these two moment arms, r/R (Fig. 1) (Biewener, 1989).

Differences in EMA change the muscle force required and thus the amount of active muscle volume required for running. Smaller EMAs require a greater muscle force to exert a specified force on the

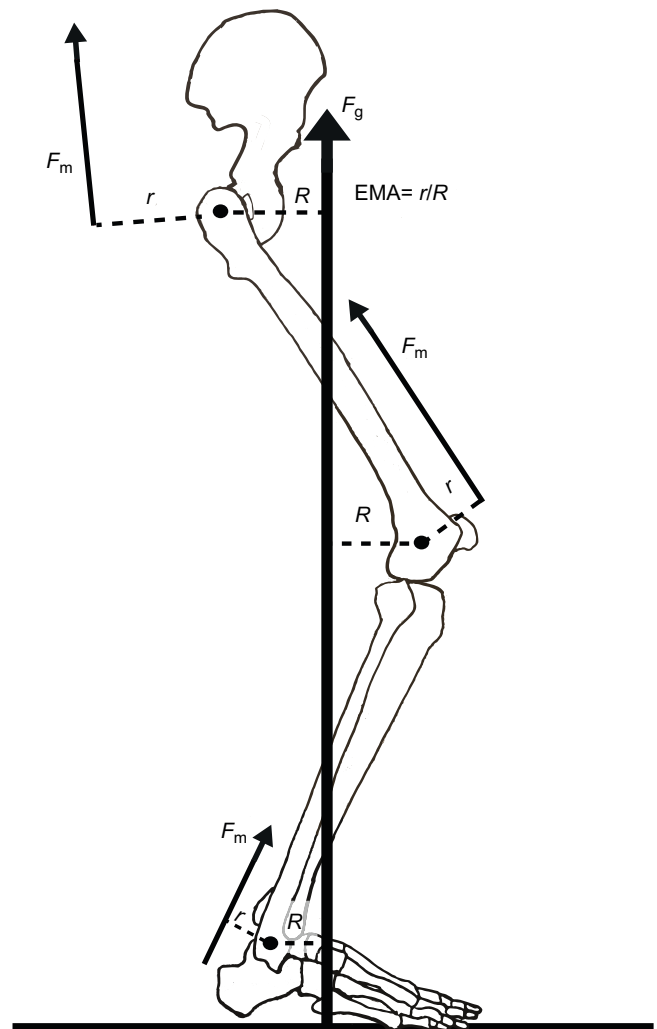


Fig. 1. Diagram of effective mechanical advantage (EMA) at the hip, knee and ankle. EMA is defined as the ratio of the muscle moment arm (r) to the resultant ground reaction force moment arm (R). F_m , muscle force; F_g , ground reaction force.

ground, which necessitates a greater volume of active muscle and thus presumably elicits greater metabolic rates. EMA is smaller when the joints are more flexed and/or less aligned with the resultant GRF. When an animal's limb posture is more upright (straighter legs), the GRF is more aligned with the joint centers and the force that the muscles must exert to support body weight is less compared with that for a bent limb posture.

Most previous versions of the cost of generating force approach have made the simplifying assumption that EMA does not change with running velocity (Kram and Taylor, 1990; Roberts et al., 1998; Pontzer, 2005, 2007, 2016; Pontzer et al., 2009a,b). Even with that assumption, Roberts et al. (1998) found that the original cost of generating force hypothesis could explain about 70% of the increase in the rate of metabolic energy consumption in humans across running velocities from 2.0 to 4.0 m s^{-1} . However, in humans there is evidence that as velocity increases, EMA decreases, and thus active muscle volume increases (Biewener et al., 2004).

Here, we performed a more systematic analysis of EMA to determine whether we could more completely explain the increase in metabolic rate across the full velocity range that human runners are capable of sustaining aerobically. Specifically, we explored

whether the remaining 30% of the increase in metabolic rate can be attributed to changes in EMA (and thus V_m). Both Griffin et al. (2003) and Pontzer et al. (2009a,b) used estimates of V_m to better predict metabolic cost in walking humans. Pontzer et al. (2009a,b) also estimated V_m to predict the metabolic rates of running bipedal dinosaurs.

Here, we took the same approach but focused on running humans. Based on isolated muscle energetics (Crow and Kushmerick, 1982; Rall, 1985), Kram and Taylor (1990) and Taylor (1994) hypothesized that metabolic rate (\dot{E}_{met} in watts) should be proportional to the product of the volume of active muscle integrated over time and the rate of force generation. They assumed that the volume of active muscle primarily acts to support body weight and that EMA is invariant across running velocity. Thus, they assumed that a given volume of active muscle exerts the same vertical force on the ground. We eschewed both of those assumptions and instead calculated V_m based on biomechanical measures. Thus, we reverted to the simple equation (Eqn 2) as outlined in Taylor (1994):

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

Our main goal was to quantify how metabolic rate, the rate of force production and active leg muscle volume change across a wide range of running velocities (8–18 km h⁻¹) in humans. We hypothesized that over the wide range of velocities tested, EMA of the lower limb joints would overall decrease, necessitating a greater volume of active muscle recruitment. We incorporated an active muscle volume term (V_m) into the original cost of generating force hypothesis (Eqn 1) and implemented a cost coefficient, k (Eqn 2). The cost coefficient k represents the amount of metabolic energy consumed (J) per cubic centimeter of active muscle volume.

Given the expected proportionality, we further hypothesized that k would be constant across running velocity, indicating that the rate of force generation and active muscle volume together can better explain the metabolic cost of running.

MATERIALS AND METHODS

Subjects

Ten high-caliber, male human distance runners participated (27.1 ± 2.5 years, 64.7 ± 4.1 kg, 179.2 ± 5.9 cm). All subjects had recently completed a sub-31 min 10 km race at sea level, a sub-32 min 10 km at the local altitude (~1655 m) or an equivalent performance in a different distance running event. Subjects gave written informed consent that followed the guidelines of the University of Colorado Boulder Institutional Review Board.

Experimental set-up and protocol

Over two visits, subjects performed a series of running trials on a motorized, force-measuring treadmill (Treadmetrix, Park City, UT, USA). During their first visit, subjects habituated to the treadmill and expired-gas equipment, while we verified that they could run sub-maximally at the three fastest velocities we planned to test (14, 16 and 18 km h⁻¹). Subjects performed 5 min running trials at each velocity and rested for 5 min between trials. To assure a primary reliance on oxidative metabolism, we measured blood lactate concentration. To do so, we obtained 50 µl of blood from the subject's finger at rest and at the completion of each 5 min trial. We analyzed blood samples in duplicate with a YSI 2300 lactate analyzer (YSI, Yellow Springs, OH, USA). Subjects who could run all three velocities with a blood lactate level below 4 mmol l⁻¹

(Heck et al., 1985) and a respiratory exchange ratio (RER) < 1.0 were deemed capable of running at all velocities sub-maximally.

Following the three 5 min running trials, we placed 40 reflective markers on the subject's legs using a modified Helen Hayes marker set. Markers were placed bilaterally on the ankle, knee and hip joint centers and clusters were placed on each segment. Subjects then ran 2 min trials at 8, 10, 12, 14, 16 and 18 km h⁻¹ in a random order with *ad libitum* rest in between. We used a 3D motion-capture system (Vicon 512 System, Oxford, UK) to determine the positions of the ankle, knee and hip joints of both legs relative to the force-measuring treadmill. The short duration of these trials for biomechanics measurements prevented marker movement due to sweat.

During a second visit, subjects arrived to the laboratory 2 h post-prandial to mitigate potential effects of diet on metabolic rate. After resting for 5 min, we measured their metabolic rate while they stood quietly. Then, each subject ran at the same six velocities as the first visit in their same randomized order as in visit one. Trials lasted 5 min for each velocity, and subjects took 5 min breaks between trials. During the standing and running trials, subjects breathed through a standard mouthpiece (Hans Rudolph 2700, Kansas City, MO, USA) and wore a nose clip, allowing us to measure their rates of oxygen uptake (\dot{V}_{O_2}) and carbon dioxide production (\dot{V}_{CO_2}) with an open-circuit expired gas analysis system (Parvomedics TrueOne 2400, Sandy, UT, USA). After completing the 6 submaximal trials, subjects recovered for 10 min and then completed a $\dot{V}_{\text{O}_2, \text{max}}$ test. For the $\dot{V}_{\text{O}_2, \text{max}}$ test, subjects ran at 16 km h⁻¹ on a level treadmill for 1 min. Then, we increased the grade by 1% each minute until subjects reached voluntary exhaustion (Daniels, 2013).

Data analyses

Physiology

Using our measured \dot{V}_{O_2} and \dot{V}_{CO_2} along with the energetic equivalents (Peronnet and Massicotte, 1991; Kipp et al., 2018), we calculated and averaged metabolic rate (\dot{E}_{met} in watts) from the last 2 min of each trial when metabolic rate had reached steady state. We defined $\dot{V}_{\text{O}_2, \text{max}}$ as the greatest 30 s mean value obtained. Our criteria for reaching $\dot{V}_{\text{O}_2, \text{max}}$ were: a plateau in oxygen consumption with an increase in workload (grade) and/or RER over 1.15 (Issekutz et al., 1962).

We calculated the traditional cost coefficient (c) for each velocity by multiplying the mean metabolic rate (\dot{E}_{met}) normalized to body weight (W_b) by t_c as proposed by Kram and Taylor (1990) (Eqn 1). Furthermore, we calculated the cost coefficient (k) by dividing metabolic rate in watts by V_m and multiplying by t_c (Eqn 2). For Eqn 1, Kram and Taylor (1990) and Roberts et al. (1998), calculated net \dot{E}_{met} by subtracting the y -intercept of the linear regression. However, for several reasons, we used gross \dot{E}_{met} , which includes all of the metabolic energy expended during running. First, baseline metabolism may or may not remain constant when running (Poole et al., 1992; Stainbsy et al., 1980). Further, the linear intercept for human runners is quite close to zero and some authors report a curvilinear relationship between metabolic rate and velocity for human runners over a wide velocity range (up to 5.14 m s⁻¹) (Stuedel-Numbers and Wall-Scheffler, 2009; Tam et al., 2012; Batliner et al., 2018; Black et al., 2017). However, we provide the average metabolic rate during standing so that others may calculate net metabolic rate if desired (Table 1).

Mechanics

We collected GRF data at 1000 Hz and kinematics data at 200 Hz during the last 30 s of each biomechanics measurement trial (Vicon 512 System) and analyzed 10 strides (20 steps). We used a

Table 1. Metabolic variables for 10 subjects across velocity

Velocity (km h ⁻¹)	\dot{V}_{O_2} (l min ⁻¹)	\dot{V}_{O_2} (ml kg ⁻¹ min ⁻¹)	RER	\dot{E}_{met} (W)	\dot{E}_{met} (W kg ⁻¹)
Standing	0.33±0.04	5.0±0.5	0.851±0.080	108.5±15.7	1.70±0.18
8	1.68±0.14	26.4±1.6	0.826±0.045	591.1±41.0	9.28±0.51
10	1.99±0.15	31.2±1.7	0.835±0.037	695.7±49.7	10.9±0.58
12	2.32±0.20	36.4±2.3	0.846±0.032	814.4±70.2	12.8±0.81
14	2.76±0.21	43.3±2.0	0.854±0.027	968.5±70.3	15.2±0.67
16	3.27±0.23	51.4±2.6	0.886±0.042	1162±77.5	18.3±1.06
18	3.81±0.28	59.8±2.9	0.937±0.044	1366±95.5	21.4±0.99

Data are means±s.d. \dot{V}_{O_2} , rate of oxygen consumption; RER, respiratory exchange ratio; \dot{E}_{met} , rate of metabolic energy consumption. We calculated both a linear fit to the gross \dot{E}_{met} normalized to body mass versus velocity v ($\dot{E}_{met}=1.22v-1.19$; $R^2=0.981$) and a more appropriate 2nd order polynomial regression ($\dot{E}_{met}=0.056v^2-0.241v+7.64$; $R^2=0.999$). Equivalent equations in $m\ s^{-1}$ are as follows: linear fit: $\dot{E}_{met}=4.38v-1.19$; 2nd order polynomial regression: $\dot{E}_{met}=0.73v^2-0.86v+7.62$.

Butterworth low-pass filter (14 Hz) to process both GRF and target-marker data (Visual 3D software, C-Motion Inc., Germantown, MD, USA) (Bisseling and Hof, 2006). We determined the touchdown and toe-off times from the vertical GRF recordings using a 30 N threshold. This allowed us to calculate stride frequency and t_c . We calculated internal joint moments using the Visual 3D software. Because measurements of the point of force application (center of pressure) are very noisy during the beginning and end of the foot-ground contact phase, we followed the methods of Griffin et al. (2003), Biewener et al. (2004) and Pontzer et al. (2009a,b) and only included joint moment ($M_{net\ joint}$) values in subsequent analysis when they exceeded 25% of their maximum value.

Using Eqn 3 we determined the net muscle force (F_m) acting at each joint during the stance phase by averaging joint moments when they were at least 25% of their maximum ($M_{net\ joint}$) and dividing by the muscle moment arm (r) (Eqn 3). We determined r by palpation of muscle attachments relative to estimates of joint centers for each subject and compared it with direct measures from cadavers (Biewener et al., 2004). Even though our measures were similar to the cadaver measurements, we opted for the more precise measurements of r taken from the cadavers:

$$F_m = M_{net\ joint}/r. \quad (3)$$

The muscle moments of the knee and hip include a flexion moment contributed by two-joint muscles that extend one joint but flex another. The gastrocnemius (gastroc) can exert a flexion moment contributing to the knee moment; the biceps femoris (bf) can exert a flexion moment contributing to the knee moment; and the rectus femoris (rf) can exert a flexion moment contributing to the hip moment. We calculated the force in the two-joint muscles by assuming that force was distributed equally across physiological cross-sectional area (A) at the joint extensor muscles:

$$M_{ankle} = r_{ankle} \cdot F_{m,ankle}, \quad (4)$$

$$M_{knee} = r_{knee} \cdot F_{m,knee} - (r_{bf} \cdot F_{m,hip} \frac{A_{bf}}{\sum A_{hip}}) - (r_{gastroc} \cdot F_{m,ankle} \cdot \frac{A_{gastroc}}{\sum A_{ankle}}), \quad (5)$$

$$M_{hip} = r_{hip} \cdot F_{m,hip} - (r_{rf} \cdot F_{m,knee} \frac{A_{rf}}{\sum A_{knee}}). \quad (6)$$

The only unknown quantities in these three equations are $F_{m,ankle}$, $F_{m,knee}$ and $F_{m,hip}$. We calculated $F_{m,ankle}$ directly from Eqn 4. Eqns 5 and 6 contain two unknowns, $F_{m,knee}$ and $F_{m,hip}$, so we solved them simultaneously.

We calculated EMA about the hip, knee and ankle joints as the ratio (r/R) of the muscle moment arm (r) to the resultant GRF moment arm (R), over the same period of the stride used to calculate F_m (Eqn 7):

$$EMA = \frac{r}{R} = \frac{GRF}{F_m}. \quad (7)$$

To estimate the volume of actively recruited muscle (V_m , cm³) per leg at each joint during stance, we used the morphological data of the lower extremity muscles of male human cadavers that were used in Biewener et al. (2004). The weighted average of fascicle length (L , cm) was determined from multiple agonist muscles. We assumed that muscles exert an isometric force per unit of cross-sectional area of active fibers (σ) of 20 N cm⁻² based on Perry et al. (1988):

$$V_m = LF_m/\sigma. \quad (8)$$

To calculate the percentage of the metabolic rate explained by $1/t_c$ alone, as well as $1/t_c$ and V_m , for each velocity tested, we compared the measured metabolic rate with the predicted metabolic rate from Eqns 1 and 2. Using the measured values for \dot{E}_{met} , $1/t_c$, V_m and W_b , we calculated c and k for each of the six velocities using Eqns 1 and 2, respectively. We then used the mean values for c and k to predict \dot{E}_{met} . At each velocity, we calculated a residual (measured metabolic rate minus predicted metabolic rate). The mean percentage difference between the residual and the measured metabolic rate indicated the increase in metabolic rate not predicted by $1/t_c$ (Eqn 1), or $1/t_c$ and V_m (Eqn 2).

Statistics

We calculated means±s.d. for all tested variables and tested for normality using the Shapiro–Wilk normality test. We performed a linear regression analysis on the cost coefficients c and k to determine whether the slopes differed significantly from zero. Additionally, we analyzed the cost coefficient k with a one-way repeated measures ANOVA at each of the velocities tested. We fitted individual subject linear and 2nd order curvilinear regressions to the metabolic rate versus velocity values and used R^2 values for each subject to assess the strength of the two regression methods. We used a paired samples t -test to compare the means of individual R^2 values for linear and curvilinear fits. We considered results significant at a $P<0.05$. We performed statistical analyses using RStudio (version 0.99.892, <https://www.rstudio.com/>) software.

RESULTS

Across the velocity range tested, 86% of the increase in metabolic rate could be accounted for by the rate of force production ($1/t_c$) alone using the mean c (Fig. 2A). Moreover, 98% of the increase in metabolic rate could be accounted for by using both $1/t_c$ and active leg

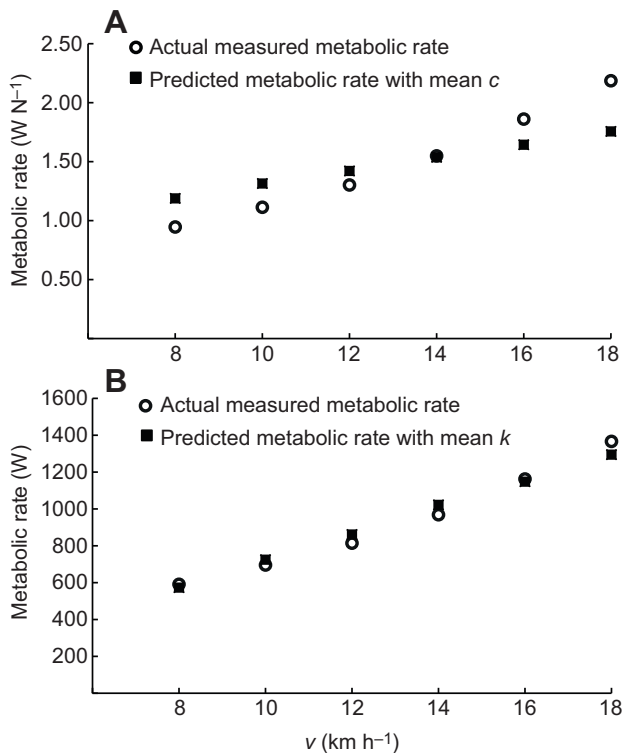


Fig. 2. Metabolic rate across velocity. (A) Measured metabolic rate and predicted metabolic rate using mean cost coefficient c versus velocity (v). (B) Measured metabolic rate and predicted metabolic rate using mean cost coefficient k versus v .

muscle volume using the mean k (Fig. 2B). Linear regression t -tests showed that the slope for c was significantly different from zero ($P < 0.001$), while the cost coefficient k was nearly constant across the velocity range (Fig. 3), with a slope not statistically different from zero ($P = 0.127$). In further support, the one-way repeated measures ANOVA revealed that the cost coefficient k was not significantly different between the different velocities ($P = 0.575$).

Every subject's gross metabolic rate increased by more than 2-fold across the velocity range. At $18 km h^{-1}$, subjects' rates of oxygen consumption averaged 82.5% of their $\dot{V}_{O_{2,max}}$ values (average $\dot{V}_{O_{2,max}} = 72.7 \pm 3.9 ml O_2 kg^{-1} min^{-1}$; range 67.6–80.3 $ml O_2 kg^{-1} min^{-1}$) or 81.4% of their \dot{E}_{max} value (average $\dot{E}_{max} = 26.3 \pm 1.4 W kg^{-1}$; range 24.4–29.3 $W kg^{-1}$) (Beck et al., 2018). Further, at $18 km h^{-1}$, average RER was 0.937 ± 0.04 , and average blood lactate concentration was $3.51 \pm 0.31 mmol l^{-1}$. No subject exceeded an RER of 1.0 or a blood lactate value of $4.0 mmol l^{-1}$. Together, these variables clearly indicate that the subjects were at a sub-maximal intensity. Standing metabolic rate was $1.70 \pm 0.18 W kg^{-1}$. Table 1 reports all metabolic variables.

Ground contact time (t_c) decreased over the velocity range and thus the rate of force production ($1/t_c$) increased. Vertical GRF peaks were greater at faster velocities (Table 2). Three of the 10 subjects transitioned from a rearfoot to a midfoot strike classification at faster velocities (14, 16 or $18 km h^{-1}$), as indicated by the disappearance of the impact peaks in the vertical GRF trace (Cavanagh and Lafortune, 1980). All other subjects maintained their same foot strike pattern over the entire range of velocities.

Mean net joint moment ($M_{net, joint}$) increased with velocity at the ankle and hip (Fig. 4). However, at the knee, $M_{net, joint}$ increased up to 14 or 16 $km h^{-1}$ and then slightly decreased (Table 3). We observed these patterns in every subject. Accordingly, over the

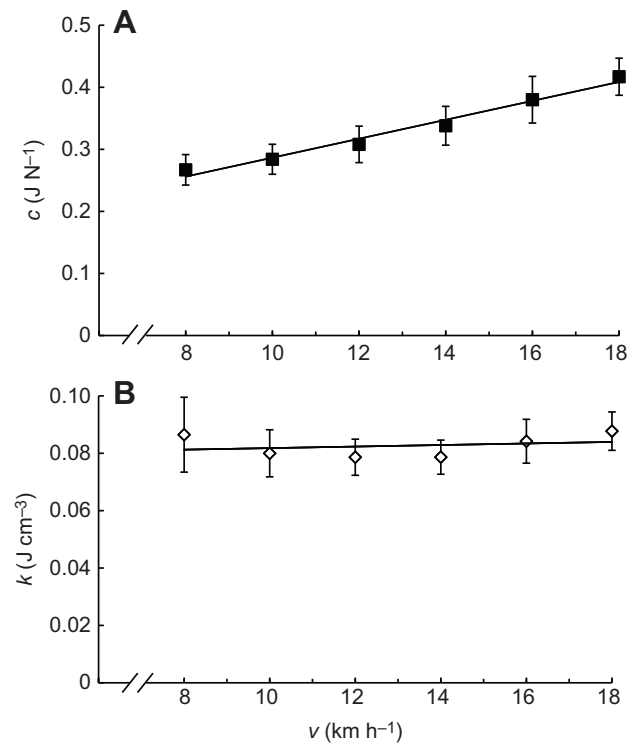


Fig. 3. Cost coefficients across velocity. The cost coefficient c (A) versus the new cost coefficient k (B), calculated using gross metabolic rate. Equations for the cost coefficients across velocity, v ($km h^{-1}$): $c = 0.0153v + 0.034$; $k = 0.0003v + 0.079$. Error bars indicate ± 1 s.d.

complete velocity range, ankle EMA decreased by $19.7 \pm 11.1\%$, knee EMA increased by $11.1 \pm 26.9\%$ and hip EMA decreased by $60.8 \pm 11.8\%$ (Fig. 5).

Total mean active muscle volume increased by $52.8 \pm 10.6\%$ across the velocity range (Fig. 6). Over the velocity range, active muscle volume increased by $60.5 \pm 20.3\%$ at the ankle, $27.5 \pm 25.3\%$ at the knee and $81.0 \pm 19.5\%$ at the hip.

DISCUSSION

We accept both of our hypotheses. Over the wide range of velocities tested, EMA of the lower limb joints overall decreased, leading to an increased volume of activated muscle. Additionally, the new cost coefficient, k , from Eqn 2 was essentially constant across the velocity range. Together, the rate of force production ($1/t_c$) and active leg muscle volume (V_m) explained 98% of the increased metabolic rate required to run at faster velocities (Fig. 2). Our average value for k ($0.079 J cm^{-3}$) is similar to the minimum k ($0.09 J cm^{-3}$) reported by Griffin et al. (2003) for human walking.

Table 2. Biomechanical variables for 10 subjects across velocity

Velocity ($km h^{-1}$)	t_c (ms)	Peak vertical GRF (N)	Peak vertical GRF (W_b)	Stride frequency (strides s^{-1})
8	280 \pm 23	1530 \pm 148	2.43 \pm 0.23	1.35 \pm 0.03
10	253 \pm 15	1593 \pm 124	2.53 \pm 0.21	1.36 \pm 0.03
12	234 \pm 16	1670 \pm 129	2.66 \pm 0.25	1.39 \pm 0.03
14	216 \pm 16	1783 \pm 156	2.83 \pm 0.28	1.42 \pm 0.05
16	202 \pm 14	1820 \pm 152	2.89 \pm 0.25	1.47 \pm 0.04
18	189 \pm 12	1895 \pm 142	3.01 \pm 0.22	1.52 \pm 0.05

Data are means \pm s.d. t_c , ground contact time; GRF, ground reaction force; W_b , body weight.

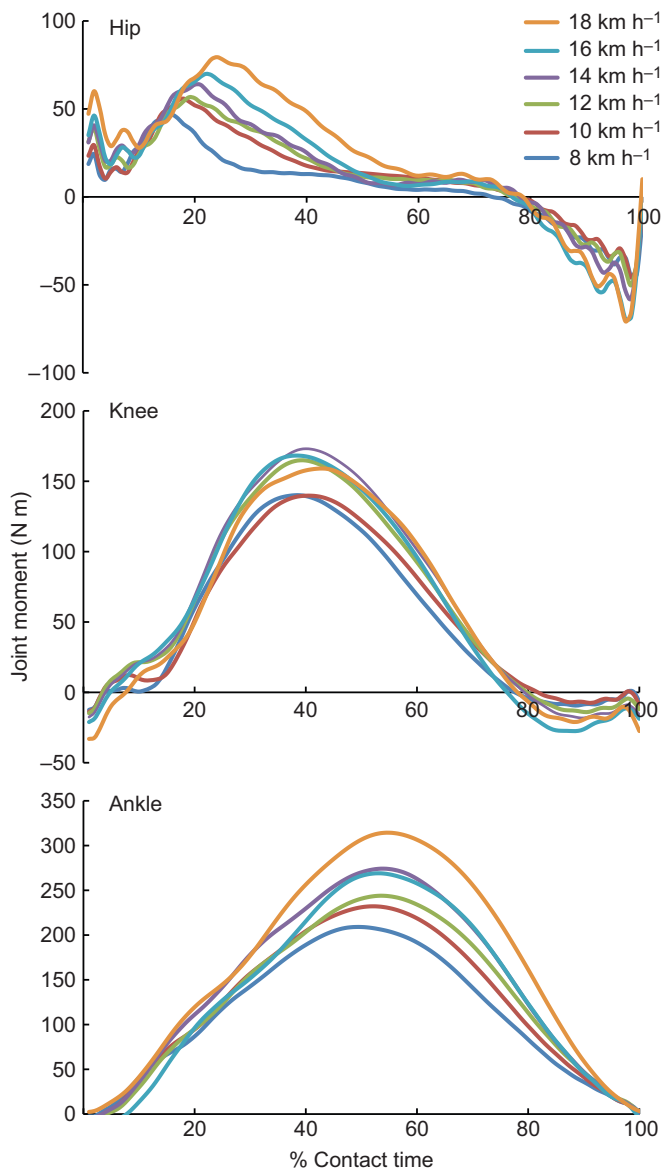


Fig. 4. Example traces of net joint moments over the velocity range at the hip, knee and ankle for a typical subject. Positive values indicate net extensor muscle moments, while negative values are net flexor muscle moments.

Further, Pontzer (2016) reported a value of 0.06 J cm^{-3} (slope of his fig. 1b) for a diverse assortment of species using both walking and running gaits. Note that Pontzer (2016) used net metabolic rate, while we use gross metabolic rate.

Table 3. Net joint moment for the ankle, knee and hip across velocity

Velocity (km h ⁻¹)	Net joint moment (N m)		
	Ankle	Knee	Hip
8	128±26	102±35	44±13
10	135±28	121±31	52±11
12	149±27	123±32	56±9
14	167±29	125±43	62±10
16	174±28	122±42	70±9
18	192±29	114±43	76±12

Net joint moment is defined as the average joint moment for the period when the moments are at least 25% of the peak joint moment at that running velocity.

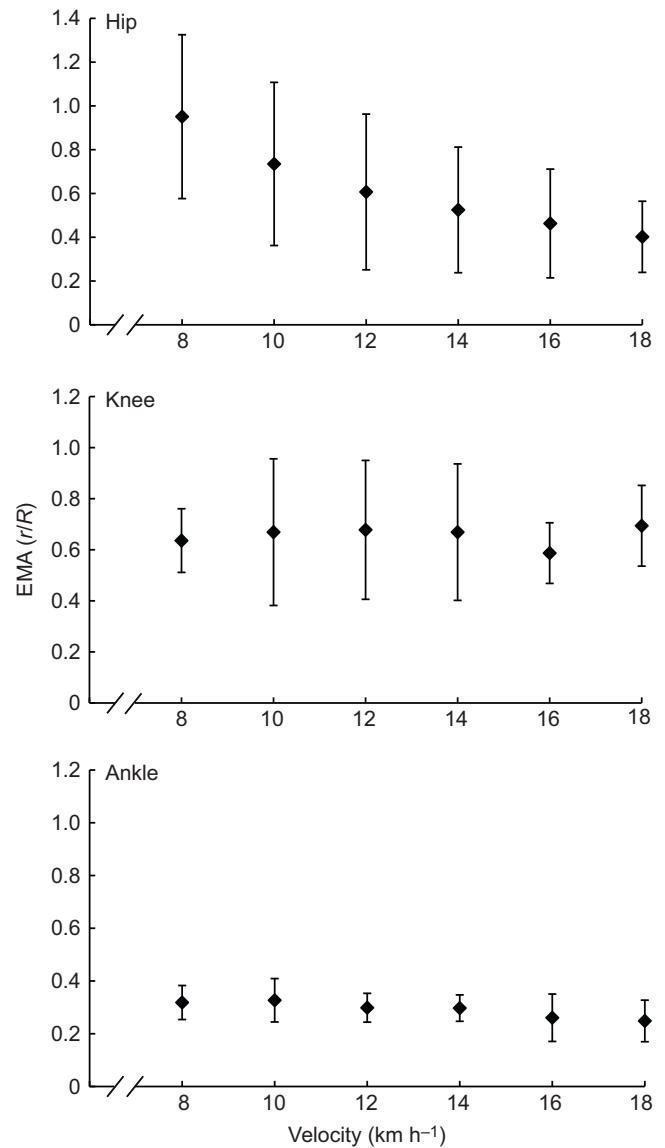


Fig. 5. EMA across velocity for hip, knee and ankle joints. Error bars indicate ± 1 s.d.

Roberts et al. (1998) found that across a narrow velocity range ($2\text{--}4 \text{ m s}^{-1}$), $1/t_c$ could account for 70% of the increase in metabolic rate in humans. Across our wider velocity range ($2.2\text{--}5.0 \text{ m s}^{-1}$), we

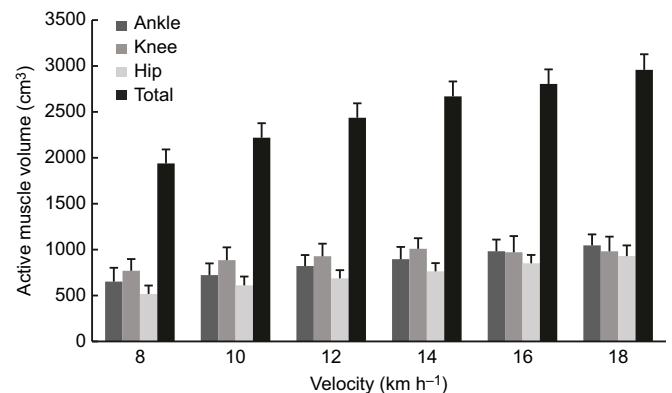


Fig. 6. Mean estimated active muscle volume per leg across velocity for ankle, knee and hip extensor muscles. Error bars indicate ± 1 s.d.

found that $1/t_c$ alone accounted for 86% of the increase in metabolic rate. We attribute this difference to the use of net metabolic rate by Roberts et al. (1998), whereas we used gross metabolic rate in our calculations. If we use our net metabolic rate data, $1/t_c$ accounts for 65% of the increase in metabolic rate across our full range of velocities, and from 8 to 14 km h⁻¹ (2.2–3.8 m s⁻¹) $1/t_c$ accounts for 78% of the increase in metabolic rate. Taken together, our findings agree with Roberts et al. (1998).

Our study builds upon previous studies that suggest that changes in the EMA of the legs influence the metabolic cost of running for humans and other species (Biewener, 1989; Full et al., 1990; McMahon et al., 1987). Here, for humans, we found that from 8 to 18 km h⁻¹, ankle EMA decreased by 19.7±11.1%, while hip EMA decreased by 60.8±11.8%. Accordingly, the ankle plantar flexor active muscle volume increased by 60.5% from 652±150 cm³ to 1046±120 cm³, while the hip extensor active muscle volume increased by 81.0% from 517±92.0 cm³ to 935±110 cm³ across the velocity range. Knee EMA increased 11.1±26.9% over the velocity range; however, active muscle volume still increased 27.5±25.3% because of the increase in the peak resultant GRF over the velocity range. Because changes in EMA of the legs influence the metabolic cost of running, it is possible that EMA could give greater insight into inter-individual variations in metabolic rate.

We observed that each subject's gross metabolic rate increased curvilinearly across the velocity range. The R^2 values for each subject's curvilinear fits for metabolic rate versus velocity (average $R^2=0.998$) were slightly but significantly greater than the R^2 values for linear fits (average $R^2=0.980$) ($P<0.05$). A linear fit of metabolic rate versus velocity resulted in a mean intercept of -1.19 W kg⁻¹ (range: -0.21 to -2.04), while a 2nd order polynomial fit of metabolic rate versus velocity resulted in a mean intercept of 7.64 W kg⁻¹ (range: 4.02 to 9.95). Our data concur with previous studies that reported a non-linear increase in metabolic rate for good human runners over a wide range of velocities (covering a velocity span that changes by at least 2.5 m s⁻¹) (Stuedel-Numbers and Wall-Scheffler, 2009; Tam et al., 2012; Batliner et al., 2018; Black et al., 2017). Kram and Taylor (1990) and Roberts et al. (1998) calculated net metabolic rate for a variety of small and large species by subtracting the y -intercept of linear regressions. However, we chose not to do this given the negative intercepts from the linear fit of our data. We believe the negative intercept is an artifact resulting from forcing a linear fit to intrinsically curvilinear data. An alternative approach is to subtract the standing metabolic rate. However, subtracting a constant from our measured metabolic rates does not change our conclusions. Overall, our data suggest that when we more fully account for the biomechanics of human running [i.e. changes in limb posture (EMA) and thus active muscle volume], the relationship between metabolic rate and velocity is better explained.

We intentionally did not consider the metabolic cost and muscular force required for swinging the legs during running. Taylor's original cost of generating force hypothesis was instigated from his earlier experiments comparing goats, gazelles and cheetahs, which were all about the same overall body mass (28.1–24.2 kg) (Taylor et al., 1974). Despite large differences in limb mass and limb mass distribution, the three species all expended about the same amount of energy to run. Taylor et al. (1974) surmised that at a constant running speed, little metabolic energy is used to accelerate and decelerate the limbs. However, as Modica and Kram (2005) recapitulated in detail, the cost of leg swing is controversial but not zero. Most relevant to the present study, Moed and Kram (2005) found that in humans, across a range of running velocities

(2–4 m s⁻¹), the relative cost of leg swing remained nearly the same modest percentage (10%) of the total metabolic rate. Thus, even though we ignored the metabolic cost of leg swing, our results are likely not confounded by an increased percentage of the total metabolic cost due to leg swing across the velocity range.

Kram and Taylor's (1990) original cost of generating force hypothesis interpreted $1/t_c$ as the rate of generating force within a step and thus reflecting the rate of cross-bridge cycling in the active muscles (see Taylor, 1994). The intrinsic rate of muscle shortening (and hence the rate of cross-bridge cycling) varies widely between muscle fibers within a given muscle (Bottinelli and Reggiani, 2000). For example, within the human vastus lateralis muscle, Bottinelli et al. (1996) found that the maximum shortening velocity spanned a 4- to 9-fold range depending on the method of determining shortening velocity. At the slowest running velocity tested in the present study, average $1/t_c$ was 3.57 s⁻¹ and at the fastest running velocity tested, average $1/t_c$ was 5.29 s⁻¹, approximately a 1.5-fold increase. The fastest human sprinters have $1/t_c$ values of ~ 10.6 s⁻¹ (Rabita et al., 2015). Thus, it appears that the factorial range of muscle shortening velocities is at least comparable to the range of $1/t_c$ across the spectrum of human running velocities.

Pontzer (Pontzer, 2007, 2016; Pontzer et al., 2009a,b) contends that $1/t_c$ primarily reflects the muscle activation–relaxation costs not cross-bridge cycling costs. Classic (Homsher et al., 1972) and contemporary (Barclay et al., 2008) muscle physiology experiments suggest that activation–deactivation costs comprise only about one-third of the total energetic cost of isometric force production. In stark contrast, other studies report that activation–deactivation comprises 80% of the cost of isometric force production (Zhang et al., 2006). As stated previously, further isolated muscle experiments are needed to resolve these disagreements.

A limitation of our study was the use of muscle moment arm, fascicle length and pennation angle data obtained from cadavers with an average age at death of 78 years. Clearly, muscles atrophy with advanced age. But fortunately, our analysis of how active muscle volume changes as a function of velocity depends only on the fascicle length and pennation angle of the muscles within the limb, which are less affected by age and muscle atrophy (Narici et al., 2003). Another potential limitation is that we assumed a constant muscle moment arm for each joint. In walking, Achilles tendon moment arms have been shown to modestly increase during plantarflexion (Rasske et al., 2017). It is possible that the muscle moment arms during running also vary during stance.

In contrast to bipedal humans, in quadrupedal mammals Biewener (1989) reported that EMA does not vary substantially with velocity or gait changes. Quadrupedal mammals that can switch between multiple gaits have shown linear increases in metabolic rate across running speeds (Taylor et al., 1970, 1982). Given our findings for bipedal humans, further research should seek to establish whether a decrease in EMA at faster velocities occurs with other bipedal species (i.e. birds) that do not switch between walking, trotting or galloping gaits like quadrupeds (Gatesy and Biewener, 1991).

In this study, we asked a simple question: why does metabolic rate increase when humans run faster? We measured the cost coefficient (k) that relates metabolic rate to the rate of force production ($1/t_c$) and the leg muscle volume activated. After quantifying those variables over a wide range of running velocities, we found that k was nearly constant, indicating that the rate of force production and active leg muscle volume together almost completely account for the metabolic requirements of human

running. Our results link the biomechanics and metabolic costs of human running with a simple equation.

Acknowledgements

We thank Bailey Kowalczyk for assisting with data collection, and Owen Beck and Wouter Hoogkamer for their help with data filtering and processing.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.K., R.K.; Methodology: S.K., A.G., R.K.; Formal analysis: S.K., R.K.; Investigation: S.K., R.K.; Resources: A.G.; Writing - original draft: S.K., R.K.; Writing - review & editing: S.K., A.G., R.K.; Supervision: A.G.

Funding

This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

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