

## RESEARCH ARTICLE

## Metabolic cost of human hopping

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## ABSTRACT

To interpret the movement strategies employed in locomotion, it is necessary to understand the source of metabolic cost. Muscles must consume metabolic energy to do work, but also must consume energy to generate force. The energy lost during steady locomotion and, hence, the amount of mechanical work muscles need to perform to replace it can be reduced and, in theory, even eliminated by elastically storing and returning some portion of this energy via the tendons. However, even if muscles do not need to perform any mechanical work, they still must generate sufficient force to tension tendons and support body weight. This study shows that the metabolic cost per hop of human hopping can largely be explained by the cost of producing force over the duration of a hop. Metabolic cost determined via oxygen consumption is compared with theoretical predictions made using a number of different cost functions that include terms for average muscle work, force, force rate and impulse (time integral of muscle force). Muscle impulse alone predicts metabolic cost per hop as well as more complex functions that include terms for muscle work, force and force rate, and explains a large portion (92%) of the variation in metabolic cost per hop. This is equivalent to 1/effective mechanical advantage, explaining a large portion (66%) of the variation in metabolic cost per time per unit body weight. This result contrasts with studies that suggest that muscle force rate or muscle force rate per time determines the metabolic cost per time of force production in other bouncing gaits such as running.

**KEY WORDS:** Energetics, Biomechanics, Work, Force, Impulse, Locomotion

## INTRODUCTION

It is necessary to understand the ways in which metabolic energy is consumed during locomotion in order to interpret how and why the limb functions as it does. Classic experiments using *in vitro* muscle preparations have shown that there is a metabolic cost associated not only with muscles doing work (Heidenhain, 1864; Fenn, 1924; Hill, 1938) but also with muscles generating force (Heidenhain, 1864; Evans and Hill, 1914; Hill, 1958). The laws of mechanics dictate that energy input is needed to perform positive mechanical work to increase the mechanical energy of the body or replace mechanical energy lost. However, the physiology of skeletal muscle dictates that chemical energy in the form of ATP is needed to activate a muscle and cycle the cross-bridges in order to produce muscular force regardless of whether the muscle performs mechanical work

(Alexander, 1991; Cavagna et al., 1977). Therefore, although muscular work during steady locomotion might, in theory, be eliminated by elastic storage and return of mechanical energy by spring-like elements such as tendons, energy must still be consumed by the leg muscles to generate force to support body weight and to tension the tendons (Roberts et al., 1997, 1998; Taylor et al., 1980; Taylor, 1985).

This study used vertical hopping as a simple model of leg function and energetics in repetitive, bouncing gaits such as running. The relationship between metabolic cost and mechanics was evaluated for a series of cost sources. It has been estimated that 35–54% of the mechanical energy of the body and limbs is stored and returned elastically in bouncing gaits in a variety of mammals, and up to 65% in humans (Ker et al., 1987; Alexander, 1982; Alexander and Vernon, 1975; Biewener et al., 1998; Cavagna et al., 1977; Roberts et al., 1997). This implies that 35–65% of the mechanical energy of the body is lost via negative work, which itself incurs some metabolic cost, and must be replaced by positive muscle work (Abbott et al., 1952; Ruina et al., 2005). Therefore, it seems reasonable to hypothesize that the metabolic cost of hopping might be described by a cost function that includes terms to account for both the cost of doing work and the cost of generating force (Alexander, 2002).


The metabolic cost per hop of doing work depends on the work actively performed by the muscles. The work that must be actively performed by the muscles is equal to the mechanical work required to move the body minus the work passively performed by the tendons. In the case of hopping, the mechanical work required to move the body will be dominated by the mechanical work required to lift the centre of mass (external work) because the work required to move the limbs relative to the centre of mass (internal work) is relatively small (Willems et al., 1995).

Previous studies indicate that the metabolic cost of producing muscle force may depend on force magnitude, force duration and frequency of activation (Dean and Kuo, 2011; Kram and Taylor, 1990; McMahon et al., 1987). Therefore, the metabolic cost per hop of producing force can probably be described by some combination of the force, force rate and time integral of force (impulse) produced by the muscles.

Direct metabolic assessment of running and similar activities (Kram and Taylor, 1990; Kram and Dawson, 1998; Saibene and Minetti, 2003; Sih and Stuhmiller, 2003) suggests that the metabolic cost per time of muscle force production is proportional to muscle force rate. This implies that metabolic cost per stride or cost per hop should be proportional to average muscle force. [These studies actually show that metabolic cost per time is proportional to ground reaction force rate. However, ground reaction force is used as a proxy for muscle force based on the assumption that an active unit volume of muscle produces the same ground reaction force. This assumption appears to be valid for a variety of quadrupeds and avian bipeds (Biewener, 1989; Roberts et al., 1998).] The rationale for this method of calculating the cost of force production is that the metabolic cost of locomotion should be primarily determined by the metabolic cost of producing the muscle force to support body

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weight as most of the work needed can be accomplished passively by tendons. Recruiting more muscle fibres (larger active muscle volume) to generate greater force or recruiting faster muscle fibres to generate a given force more quickly will consume more energy per stride or energy per hop.

Other studies suggest that the metabolic cost per time of producing force is proportional to force rate per time (Dean and Kuo, 2011; Doke and Kuo, 2007). This implies that metabolic cost per stride or cost per hop should be proportional to average muscle force rate. The rationale for this method of calculating the cost of force production is that metabolic cost per stride or cost per hop should be largely determined by the energy needed to pump calcium ions. More calcium must be pumped to generate more forceful or more frequent contractions because of the muscle activation and deactivation time constants and this requires more energy per stride or energy per hop (Chasiotis et al., 1987; Hogan et al., 1998).

Still others suggest that the metabolic cost per stride of producing force should be proportional to muscle impulse (the integral of muscle force with respect to time) (McMahon et al., 1987; Stainsby and Fales, 1973). The rationale for this method of calculating the cost of force production is that recruiting more muscle fibres (larger active muscle volume) to generate greater force and sustaining this force for a longer period of time should use more energy per stride or energy per hop (see, for instance, Pontzer, 2007).

The current study compared the predictions of a number of candidate cost functions with experimental metabolic cost data to determine the key biomechanical factors that influence the metabolic cost of human hopping. The cost functions consist of various combinations of terms to account for the cost per hop of muscle work, force, force rate and impulse.

## MATERIALS AND METHODS

The data analysed in this study were collected for a previous study investigating how hop height and frequency selection are influenced by optimization of metabolic cost under various testing conditions (Gutmann and Bertram, 2013). A detailed description of the methods may be found in that report. However, for the sake of completeness, a brief summary is given here.

### Ethical approval

All testing was conducted according to the protocol approved by the Conjoint Health Research Ethics Board, University of Calgary. Informed consent was obtained in writing from each subject prior to testing, according to the standards set by the latest revision of the Declaration of Helsinki.

### Subjects

Six healthy subjects (three females and three males) participated in the study. All subjects regularly engaged in strenuous aerobic exercise, i.e. at least 30 min three times per week of running, cycling, aerobics, etc. The physical characteristics of the subjects are given in Table 1.

### General protocol

Subjects were instructed to hop in place on both feet with arms held loosely at their sides. Subjects hopped for 4 min per trial while ground reaction force and metabolic gas exchange were recorded. Subjects hopped under five different testing conditions: (i) frequency-constrained conditions where hop frequency was specified but subjects were free to select their preferred hop height, (ii) height-constrained conditions where hop height was specified but subjects were free to select their preferred hop

**Table 1. Physical characteristics and number of trials successfully completed for each subject**

Subject	Sex	Age (years)	Mass (kg)	No. of trials completed
1	f	26	54.0	47
2	f	29	60.7	44
3	f	29	53.1	39
4	m	24	87.3	47
5	m	27	72.0	46
6	m	33	89.0	47

frequency, (iii) speed-constrained conditions where hop ‘speed’ (product of frequency and height) was specified but subjects were free to select their preferred frequency (or, equivalently, hop height), (iv) fully constrained conditions where both hop frequency and hop height were specified, and (v) unconstrained conditions where neither hop frequency nor hop height was specified. Hop frequency was specified by having subjects hop to the beat of a metronome. Hop height and hop speed were specified by having subjects respond to visual hop height feedback displayed on a computer screen.

Subjects did not appear to use different coordination strategies when hopping under different testing conditions, so we pooled the data from all five testing conditions to maximize the number of data points available for the current study. The total number of trials each subject completed is given in Table 1. The resulting cost surface was fairly smooth, i.e. without large jumps between neighbouring data points collected under different testing conditions, which suggested that the underlying relationship between mechanical work, force production and metabolic cost was the same regardless of testing condition.

### Mechanical variables

Force plate data were analysed after testing to obtain average values for hop period ( $T$ ), hop frequency ( $f=1/T$ ), maximum total vertical displacement of the centre of mass ( $h$ ), time spent in the air ( $t_a$ ), time spent on the ground (i.e. contact time,  $t_c$ ), vertical displacement of the centre of mass while in the air ( $h_a$ ) and vertical displacement of the centre of mass while on the ground ( $h_c$ ) for each trial. The vertical position of the centre of mass was calculated by integrating the vertical acceleration of the centre of mass twice while applying the correction algorithm described in detail in the supplementary material for Gutmann and Bertram (2013).  $h$  was calculated as the difference between the maximum and minimum vertical positions;  $T$  was calculated as the time difference between successive force maxima;  $t_a$  was calculated by finding the time period during which the ground reaction force equalled zero;  $t_c$ ,  $h_a$ , and  $h_c$  were calculated as  $t_c=T-t_a$ ,  $h_a=g t_a^2/8$  and  $h_c=h-h_a$ , respectively, where  $g$  is the acceleration due to gravity,  $9.8 \text{ m s}^{-2}$ .

### Muscle variables

A number of candidate cost functions that consisted of linear combinations of muscle variables, i.e. average muscle force, muscle force rate, muscle impulse and muscle work=external work–tendon work, were evaluated. We calculated muscle variables from the mechanical variables obtained from force plate data (see above) according to the equations described below.

Average ground reaction force must support body weight over the course of a complete hop (where centre of mass height is equal at the beginning and end of the cycle), so ground reaction force impulse must equal the impulse due to body weight,  $F_{\text{ground,ave}} \times t_c = mgT$ . Rearranging this equation yields the equation for average ground

reaction force during ground contact in body weight,  $F_G$ :

$$F_G = F_{\text{ground,ave}}/mg = T/t_c. \quad (1)$$

Average muscle force was estimated using a simple segmented-leg model (McMahon et al., 1987) (Fig. 1A). This model was chosen because it was the simplest model that could be used to describe the general relationship between joint angle,  $\theta$ , and muscle force,  $F_M$ . Balancing moments acting about the knee joint (assuming that the inertia of the shank is small compared with that of the body so that the change in angular momentum of the lower leg is negligible; Fig. 1B) and using the geometry of the model yields:

$$F_M = F_G \cdot (l/2r) \cos \theta = F_G \cdot (l/2r) \sqrt{1 - (d/l)^2}, \quad (2A)$$

where  $r$  is the length of the muscle lever arm,  $l$  is the length of the leg, and  $d$  is the minimum distance from the ground to the center of mass. This can equivalently be written as:

$$\begin{aligned} F_M &= (T/t_c)(l/2r) \cos \theta \\ &= (T/t_c)(l/2r) \sqrt{2h_c/l - (h_c/l)^2}. \end{aligned} \quad (2B)$$

In our calculations, we used  $l/2r=10$  based on a muscle lever arm of  $r \approx 0.05$  m and a leg length of  $l \approx 1.00$  m for a 1.85 m tall subject. However, the exact value of this ratio is not important because any errors in this value will be compensated for by adjusting the value of the muscle force coefficient in the cost function equations. It is more important that this ratio is constant across subjects. This should be more or less true as  $r$  and  $l$  should both scale roughly with height.

Average muscle force rate ( $R_M$ ) was calculated by dividing average muscle force (Eqn 2) by hop period,  $T$ . This yields:

$$\begin{aligned} R_M &= F_M/T = (1/t_c)(l/2r) \cos \theta \\ &= (1/t_c)(l/2r) \sqrt{2h_c/l - (h_c/l)^2}. \end{aligned} \quad (3)$$

The equation for muscle impulse ( $I_M$ ) was calculated by integrating

muscle force over the duration of a hop, which yields:

$$\begin{aligned} I_M &= \int F_{\text{muscle}} dt / mg = F_M t_c = F_G t_c (l/2r) \cos \theta \\ &= T(l/2r) \cos \theta = T(l/2r) \sqrt{2h_c/l - (h_c/l)^2}. \end{aligned} \quad (4)$$

External work ( $W_G$ ) was calculated as the amount of work done to lift the centre of mass against the force of gravity normalized by body weight:

$$W_G = mgh/mg = h. \quad (5)$$

The active muscle work ( $W_M$ ) done during each hop is roughly equal to the external work minus the work passively done by the tendons ( $W_T$ ):

$$W_M = W_G - W_T, \quad (6)$$

assuming that the internal work needed to move the limbs relative to the centre of mass is small. This has been shown to be the case for running except at the highest running speeds (Willems et al., 1995) and should be even more reasonable for hopping, where there is no protraction or retraction of the leg in each cycle.

Assuming that the tendons stretch in an approximately linear manner such that  $F_{\text{tendon}} = k_T \Delta x_{\text{max}}$ , where  $F_{\text{tendon}}$  is instantaneous tendon force,  $k_T$  is tendon stiffness and  $\Delta x_{\text{max}}$  is the maximum change in tendon length, the work passively done by the tendons is:

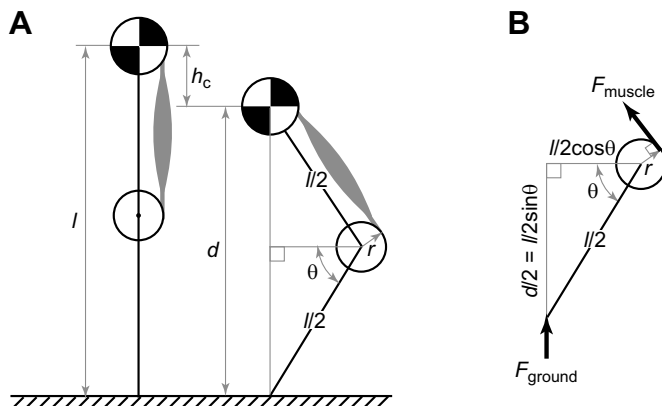
$$W_T = 1/2 \cdot k_T \Delta x_{\text{max}}^2 = 1/(2k_T) \cdot F_{\text{muscle,max}}^2, \quad (7A)$$

where the subscript ‘max’ indicates maximum force. Note that tendon force must equal muscle force because the tendon and the muscle are in series. This can be simplified to:

$$W_T = bF_M^2, \quad (7B)$$

as maximum muscle force,  $F_{\text{muscle,max}}$ , should be approximately proportional to average muscle force,  $F_M$ . In our calculations, we did not assign a value to the constant  $b$ , but instead combined  $b$  with the regression constant  $a_i$  to get the constant  $c$  preceding the muscle work term:

$$a_i W_T = (a_i b) F_M^2 = c F_M^2. \quad (7C)$$



**Fig. 1. A simple segmented-leg model.** (A) The relationship between shank (or thigh) angle,  $\theta$ , and the vertical displacement of the centre of mass during ground contact,  $h_c$ . (B) The relationship between ground reaction force,  $F_{\text{ground}}$ , and muscle force,  $F_{\text{muscle}}$  (McMahon et al., 1987).  $d$ , the minimum distance from the ground to the center of mass;  $l$ , leg length;  $r$ , muscle lever arm.

## RESULTS

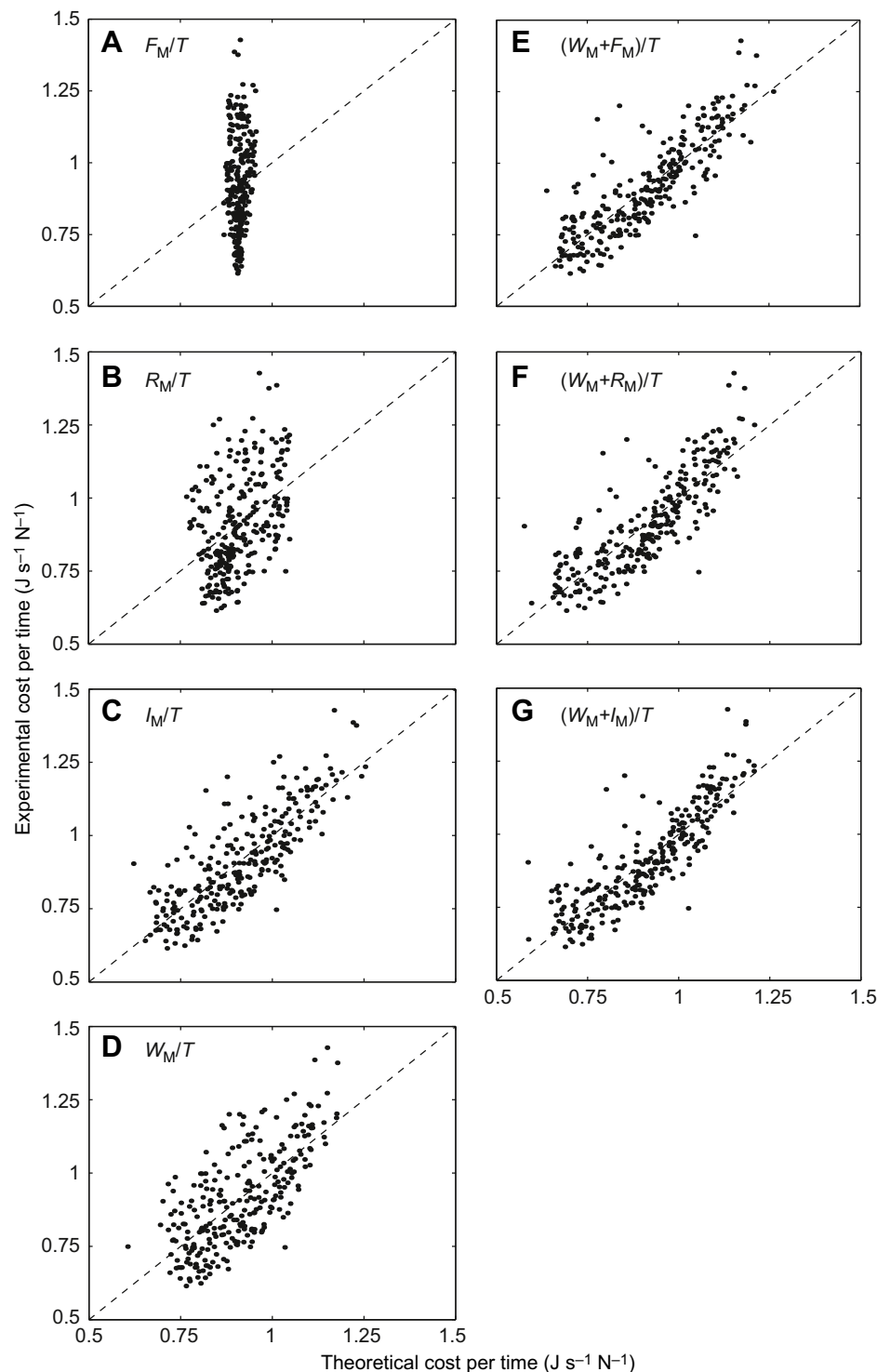
The candidate cost functions (composed of linear combinations of muscle variables per time) were fitted to the metabolic cost per time data using least squares regression. Cost functions were fitted to the cost per time version of metabolic cost so that the constant  $a_0$  in the regression would correspond to a constant resting metabolic rate (the metabolic rate when muscle work and muscle force equal zero) that is independent of hop height or hop frequency. For example, if the cost functions were fitted for the cost per hop case, resting metabolic rate would be given by  $a_0 f$  as we would need to multiply the whole metabolic cost per hop equation by  $f$  to get metabolic cost per time. Similarly, if the cost functions were fitted for the cost per height case, resting metabolic rate would be given by  $a_0 h/f$ . Coefficients,  $R^2$ -values and  $P$ -values are reported for each candidate cost function (Table 2,  $P$ -values are described in the table legend). All statistical analyses were done in Matlab (Matlab 7.12.0, The MathWorks, Inc., Natick, MA, USA). Experimentally measured metabolic cost was plotted as a function of theoretically predicted

metabolic cost for visual comparison of the predictive value of each model (Fig. 2).

The muscle force and muscle force rate models were rejected because of their low  $R^2$ -values ( $R^2=0.0117$  and  $0.165$ , respectively). The muscle force+muscle work, muscle force rate+muscle work and muscle impulse+muscle work models were rejected despite relative high  $R^2$ -values because some of the coefficients in these models were negative. The muscle force rate model also had a negative coefficient. Negative coefficients indicate that doing work or

producing force generates rather than consumes metabolic energy, which is physiologically unrealistic.

To more completely evaluate the muscle impulse and muscle work models, experimentally measured metabolic cost was plotted as a function of theoretically predicted metabolic cost for all three versions of metabolic cost for these two models (Fig. 3). The  $R^2$ - and  $P$ -values were calculated for each version of metabolic cost (Table 3). We also compared experimentally measured and theoretically predicted metabolic cost contours to visualize how



**Fig. 2. Experimentally measured metabolic cost per time as a function of theoretically predicted metabolic cost per time for the different models.** (A) The muscle force ( $F_M$ ) model. (B) The muscle force rate ( $R_M$ ) model. (C) The muscle impulse ( $I_M$ ) model. (D) The muscle work ( $W_M$ ) model. (E) The muscle work+muscle force model. (F) The muscle work+muscle force rate model. (G) The muscle work+muscle impulse model.  $T$ , hop period.



Table 2. Coefficients,  $a_i$  and  $R^2$  values for candidate cost functions

Model	Theoretical equation for metabolic cost per time	$a_0$	$a_1$	$a_2$	$a_3$	$R^2$
Muscle force	$C_{MF}/\text{time}=a_0+a_1F_M/T$	0.822	0.00647	–	–	0.0117
Muscle force rate	$C_{MR}/\text{time}=a_0+a_1R_M/T$	1.133	–0.00712	–	–	0.165
Muscle impulse	$C_{MI}/\text{time}=a_0+a_1I_M/T$	0.0673	0.188	–	–	0.655
Muscle work	$C_{MW}/\text{time}=a_0+a_1W_G/T-a_2W_T/T$	0.298	3.024	0.00263	–	0.481
Muscle work+muscle force	$C_{MW+MF}/\text{time}=a_0+a_1W_G/T-a_2W_T/T+a_3F_M/T$	1.126	1.076	–0.00576	–0.0735	0.700
Muscle work+muscle force rate	$C_{MW+MR}/\text{time}=a_0+a_1W_G/T-a_2W_T/T+a_3R_M/T$	0.879	0.647	–0.00255	–0.0113	0.683
Muscle work+muscle impulse	$C_{MW+MI}/\text{time}=a_0+a_1W_G/T-a_2W_T/T+a_3I_M/T$	0.0579	–2.840	–0.00467	0.277	0.731

These cost functions give metabolic cost per hop per body weight ( $\text{J hop}^{-1} \text{N}^{-1}$ ).  $P<0.05$  for each coefficient except for  $a_1$  in the muscle force model ( $P=0.0787$ ), indicating that there is a significant relationship between the muscle variables and metabolic cost per time except in the case of muscle force in the muscle force model.

well the different cost functions predicted metabolic cost over the full range of hop heights and frequencies that subjects could sustain for the 4 min metabolic trials (Fig. 4). Surfaces were fitted to the metabolic cost data and cost contours were created from these surfaces using the interactive surface fitting tool ‘sftool’, available in Matlab’s curve and surface fitting toolbox (Matlab 7.12.0, The MathWorks, Inc.). Although it may seem redundant to consider all three versions of the cost function, it is important to do so because each version of each muscle variable does not correlate with each version of metabolic cost equally well. For example, external work alone could explain the variation in metabolic cost per hop ( $R^2=0.731$ ) but could not explain any of the variation in metabolic cost per height ( $R^2=0$ ). This is because external work per height,  $mgh/h=mg$ , is constant, but experimentally measured

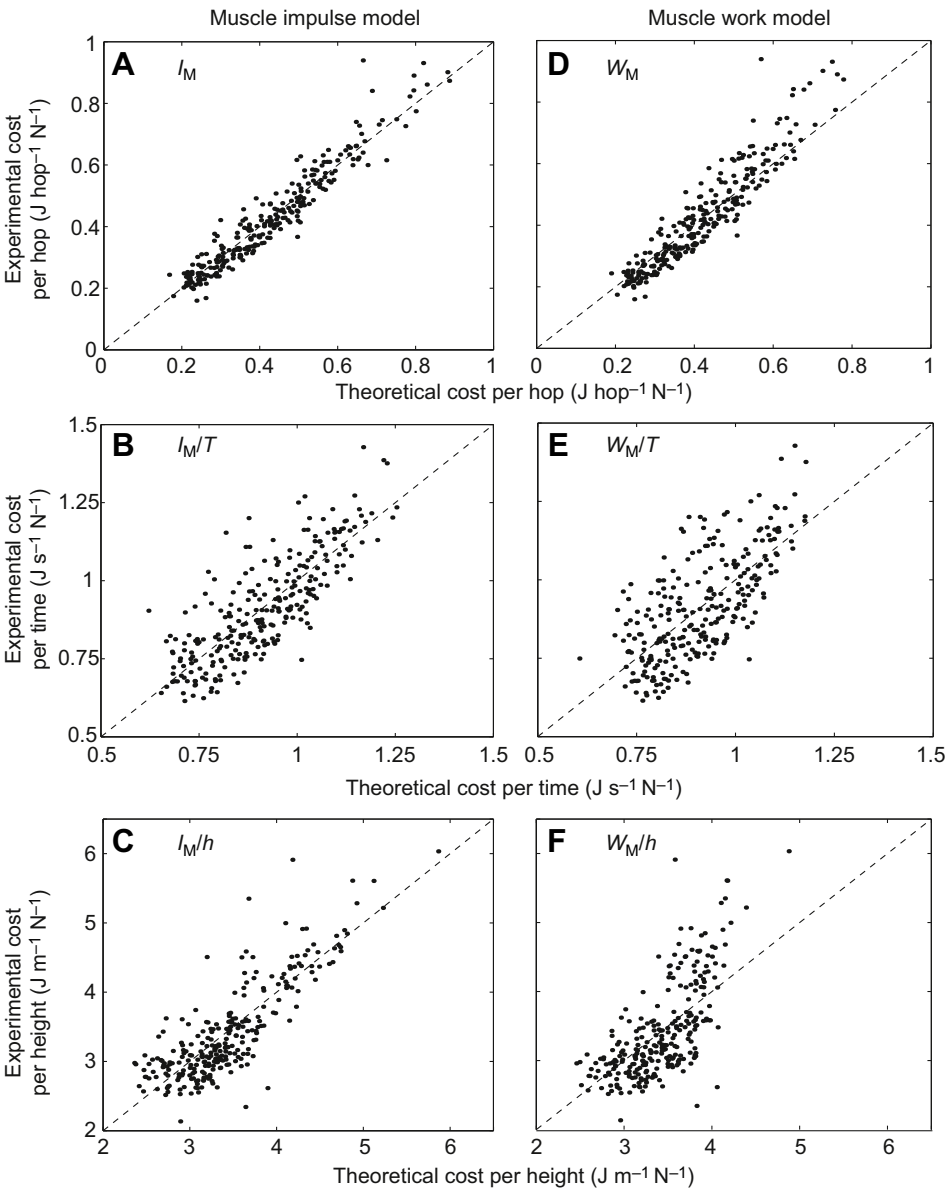


Fig. 3. Experimentally measured metabolic cost as a function of theoretically predicted metabolic cost. (A–C) The muscle impulse model and (D–F) the muscle work model. (A,D) Metabolic cost per hop, (B,E) metabolic cost per time ( $T$ ) and (C,F) metabolic cost per height ( $h$ ). If the theoretical cost function fitted the experimental metabolic data perfectly ( $R^2=1$ ), the data points would fall along the line  $y=x$  (dashed line).

**Table 3.**  $R^2$ - and  $P$ -values for plots of experimental metabolic cost versus theoretical metabolic cost for the muscle impulse,  $I_M$ , and muscle work,  $W_M$ , models

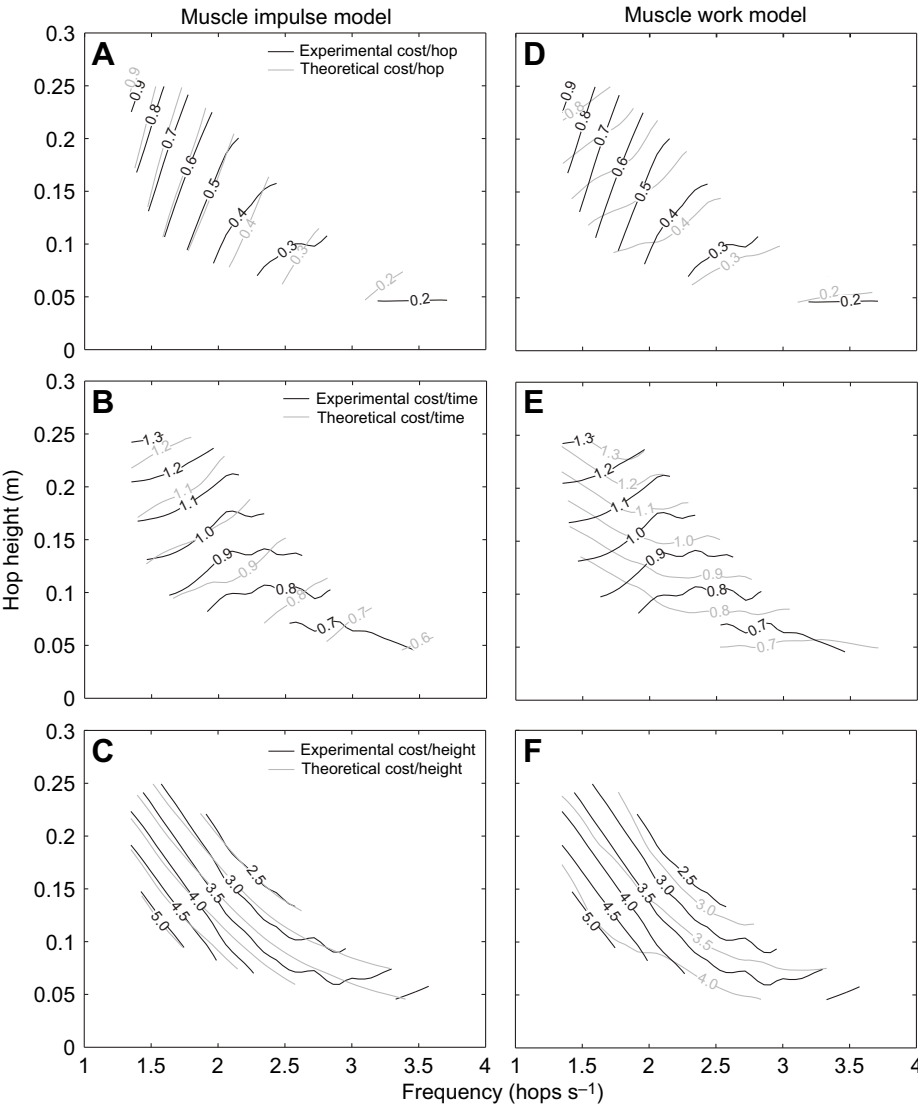
Experimental cost per hop			Experimental cost per time			Experimental cost per height		
Theoretical model/hop	$R^2$	$P$	Theoretical model/time	$R^2$	$P$	Theoretical model/height	$R^2$	$P$
$I_M$	0.922	$<10^{-4}$	$I_M/T$	0.655	$<10^{-4}$	$I_M/h$	0.687	$<10^{-4}$
$W_M$	0.876	$<10^{-4}$	$W_M/T$	0.486	$<10^{-4}$	$W_M/h$	0.481	$<10^{-4}$

Statistics are given for three different versions of metabolic cost.

metabolic cost per height triples ( $2\text{--}6\text{ J m}^{-1}\text{ N}^{-1}$ ) over the range of height–frequency combination measured. However, the dominant source of cost should provide predictive value in all three circumstances.

Although both the muscle impulse and the muscle work models fit the experimental metabolic cost per hop data quite well, the muscle work model does not fit the metabolic cost per height data as well as the muscle impulse model. This is evident from the metabolic cost scatter plots, the  $R^2$ -values and the metabolic cost contour graphs. The plot of metabolic cost per hop is quite linear for both models and theoretically predicted values of metabolic cost per hop span basically the same range of values as the experimentally

measured metabolic values ( $0.2\text{--}0.9\text{ J hop}^{-1}\text{ N}^{-1}$ ). In contrast, the plot of metabolic cost per height is highly non-linear, and the theoretically predicted values of metabolic cost per height do not span the full range of experimentally measured values (Fig. 3F). Values ranged from 2 to  $6\text{ J m}^{-1}\text{ N}^{-1}$  for experimental metabolic cost per height but only from 2 to  $4\text{ J m}^{-1}\text{ N}^{-1}$  for theoretical metabolic cost per height for the muscle work model. The  $R^2$ -values for the muscle impulse and muscle work models are 0.922 and 0.876, respectively, for metabolic cost per hop but 0.687 and 0.481 for metabolic cost per height. Although the muscle work model explains 95% ( $0.876/0.922=0.95$ ) as much variation in metabolic cost per hop as the muscle impulse model, the muscle work model



**Fig. 4.** Comparison of experimental (black lines) and theoretical metabolic cost contours (grey lines). Contours were calculated using: (A–C) the muscle impulse model and (D–F) the muscle work model for (A,D) metabolic cost per hop ( $\text{J hop}^{-1}\text{ N}^{-1}$ ), (B,E) metabolic cost per time ( $\text{J s}^{-1}\text{ N}^{-1}$ ) and (C,F) metabolic cost per height ( $\text{J m}^{-1}\text{ N}^{-1}$ ). The contour lines show how the different forms of metabolic cost vary with hop height and frequency. The theoretical cost contours match the experimental cost contours more closely in terms of both shape and range of values for the muscle impulse model.

only explains 70% ( $0.481/0.687=0.70$ ) as much variation in metabolic cost per height as the muscle impulse model. Also, the cost contours from the muscle impulse model more closely follow the experimental cost contours. For example, the experimental cost contours for metabolic cost per time generally have a positive slope. The theoretical cost contours for the muscle impulse model generally have a positive slope as well, but the theoretical cost contours for the muscle work model generally have a negative slope. Therefore, the muscle impulse model does an overall better job of predicting metabolic cost than the muscle work model.

## DISCUSSION

Statistical and graphical comparison of the experimental and theoretical metabolic cost data suggest that the metabolic cost of human hopping is determined primarily by muscle impulse. The muscle work model does a reasonably good job of predicting the variation in metabolic cost per hop and metabolic cost per time, but does not predict metabolic cost per height nearly as well as the muscle impulse model. Muscle force and muscle force rate do a rather poor job of predicting all three versions of metabolic cost. Although the muscle work+muscle force, muscle work+muscle force rate, and muscle work+muscle impulse models do a good job of predicting metabolic cost per hop, they require physiologically unrealistic constants to achieve a good fit. Therefore, these models are not acceptable.

Why should metabolic cost per hop depend primarily on muscle impulse? Previous studies show that animals and humans hold certain leg muscles nearly isometric during steady-state running and hopping and that these muscles tension tendons which store and return elastic strain energy (Biewener et al., 1998; Lichtwark and Wilson, 2005; Roberts et al., 1997). For nearly isometric contractions such as these, the cost of muscle work would probably be low (unless the relative cost of doing work was much higher than the cost of producing force) and metabolic cost would be dominated by the cost of producing muscle force. The cost associated with the muscle impulse is derived from producing a given magnitude of force over a given time period. Alexander (1991) argues that the metabolic cost of operating muscles in an optimal but non-isometric manner should be proportional to the cost of producing the same pattern of force isometrically. If this is the case, it would probably be impossible to distinguish between nearly isometric contractions that do little work and non-isometric but optimal contractions that do a substantial amount of work based on metabolic cost.

Still, it is interesting to consider why humans and other animals might try to hold their muscles nearly isometric. There is substantial evidence that humans and other animals choose to move from place to place in a way that minimizes metabolic cost per distance travelled (Alexander, 1989; Bertram, 2005; Hoyt and Taylor, 1981; Pontzer, 2007; Srinivasan and Ruina, 2006). Thus, it follows that they would try to reduce muscle activity that incurs a metabolic cost. But why should they choose to minimize work by holding muscles isometric as opposed to minimizing muscle impulse or some other measure of force production, such as force or force rate, as both muscle work and muscle force production exact a metabolic cost? Physiological arguments (Alexander, 1991) and optimizations performed using simple bipedal models (Srinivasan, 2011) suggest that minimizing work minimizes metabolic cost even in cases where metabolic cost depends on some measure of force production rather than work. However, an ironic consequence of this finding is that because minimizing work minimizes metabolic cost, measured metabolic cost will primarily be influenced by other

factors, e.g. muscle impulse, that are not so rigorously minimized (Srinivasan, 2011). This suggests that animals might use a two-part strategy to minimize metabolic cost. They might first select the gait that minimizes work in order to obtain the most dramatic cost savings, but then choose gait parameters that minimize muscle impulse in order to fine-tune their gait to achieve optimal economy. This would explain the observation that humans hold certain muscles nearly isometric while hopping (Lichtwark and Wilson, 2005), yet prefer to hop as high as possible at a given frequency to minimize muscle impulse rather than hopping as low as possible to minimize muscle work (Gutmann and Bertram, 2013).

Why use muscle impulse to quantify the cost of producing force rather than muscle work, muscle force, muscle force rate or some combination thereof? On a practical level, muscle impulse does the best job of predicting metabolic cost per hop (and muscle impulse per time and muscle impulse per height do the best job of predicting metabolic cost per time and metabolic cost per height, respectively; Table 3 and Fig. 3). Additionally, other locomotion studies point to the relationship between metabolic cost and muscle impulse (Biewener et al., 2004; McMahon et al., 1987). Increasing the bend in the knees while running increases the metabolic cost per time even though it decreases the amount of work done to lift the centre of mass. In this gait, the increase in metabolic cost per time is proportional to muscle impulse per time (McMahon et al., 1987).

We can see that by dividing the equation for muscle impulse (Eqn 4) by hop period, muscle impulse per time and, therefore, metabolic cost per time scale nearly inversely to effective mechanical advantage of the knee,  $EMA=r/(l/2\cos\theta)$  (effective mechanical advantage is defined as the ratio of joint extensor moment arm to ground reaction force moment arm for a given joint; Biewener, 1989). For human hopping, effective mechanical advantage is determined predominantly by knee angle. The shank is relatively long compared with the foot (shank length  $\sim 2 \times$  foot length) so the ground reaction force moment arm about the knee is much larger than the moment arm about the ankle. The deeper the bend at the knee (smaller  $\theta$ ), the higher the muscle force and, therefore, the larger the active volume of knee extensor muscle needed to support body weight (Biewener et al., 2004). The larger the active muscle volume, the greater the metabolic cost per time. This coincides with our perception that doing a wall-sit (statically ‘sitting’ with the back up against a wall and the knees bent at a right angle) demands more of our muscles metabolically than standing with legs straight.

Muscle force has been considered to be the primary factor responsible for determining the metabolic cost per stride for running (Kram and Taylor, 1990) and various other activities (Kram and Dawson, 1998; Saibene and Minetti, 2003; Sih and Stuhmiller, 2003). (This is equivalent to muscle force per time being the primary factor responsible for determining metabolic cost per time.) It is surprising, then, that muscle force does not do a good job at predicting the metabolic cost per hop of hopping, because the basic action of the limb – flexing and extending as load is applied and released – is quite similar for the two activities. The fact that muscle impulse is a superior predictor of metabolic cost per hop may indicate that the duration of force application (contact time) plays an important role in determining metabolic cost per hop for human hopping, as muscle impulse only differs from average muscle force by a factor of  $t_c$ :  $I_M=F_M t_c$ . However, this raises the question: why does muscle impulse appear to be not directly related to the metabolic cost of running? The arguments and evidence regarding the solution to this apparent paradox are more involved than can be described in this paper, but we have

addressed this issue in our related short communication (Gutmann and Bertram, 2017).

It is also somewhat surprising that the muscle work+muscle force rate model was rejected as a result of physiologically unrealistic constants, as force rate seems to explain the metabolic cost per bounce (or, equivalently, muscle force rate per time seems to explain the metabolic cost per time) of cyclic force production for bouncing tasks where work rate is held constant (Dean and Kuo, 2011). The contribution of muscle force rate to metabolic cost per hop is large at high frequencies for a given muscle force,  $R_M = F_M/T = F_M f$ , but the contribution of muscle impulse tends to be large at low frequencies for a given muscle force,  $I_M = F_M t_c = F_M \delta T = F_M \delta / f$ , where  $\delta = t_c/T$  is duty factor. This is one possible reason why muscle force rate might appear to be an important determinant of metabolic cost per bounce but does not appear to be an important determinant of metabolic cost per hop in the current study. It is likely that muscle force rate only becomes an important determinant of metabolic cost for frequencies higher than those used in our study. This explanation is supported by the observation that muscle force rate per time only makes a substantial contribution to total metabolic cost per time for frequencies greater than 3 bounces  $s^{-1}$  in the bouncing study (Dean and Kuo, 2011), but the majority of our data were collected at lower frequencies.

We concede that the segmented-leg model used in this study is exceedingly simple, omitting many details of leg and muscle–tendon mechanics, and therefore does not accurately reproduce the nuanced functioning of a real human leg. For example, our model only has a knee joint, so it cannot provide any insight into how humans coordinate flexion and extension of the hip, knee and ankle joints during hopping or how use of different gearing patterns affects force and work production at each joint. Likewise, because our model only has one muscle–tendon unit, it cannot provide insight into which specific muscles in the human leg are performing work and/or producing force and which tendons are storing and returning elastic strain energy at any given instant during hopping.

However, like other simple models successfully used in previous studies (Kram and Taylor, 1990; McMahon and Cheng, 1990; McMahon et al., 1987; Srinivasan and Ruina, 2006), our model still captures certain critical aspects of leg and muscle–tendon mechanics. For example, our model accounts for the fact that a muscle must generate more tension to produce a given vertical ground reaction force when a joint is flexed and a tendon can store and return more energy after it has been stretched a greater distance. Therefore, our model is still able to shed light on the relationship between basic leg and muscle–tendon mechanics and whole-body metabolic cost for human hopping. We hope that this study inspires more detailed musculoskeletal modelling that integrates joint kinematics, electromyography and ultrasound imaging of muscles (Waugh et al., 2017) to provide a detailed picture of how muscle–tendon mechanics determines metabolic cost for individual muscles in hopping, running and other bouncing gaits.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

A.K.G. arrived at the ideas presented in this manuscript based on conversations with J.E.A.B. The authors participated equally in the design of the study. A.K.G. collected and analysed hopping data. J.E.A.B. provided instruction and technical assistance

with data collection. The authors participated equally in writing and editing the manuscript.

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#### Data availability

Data are available from University of Calgary Dataverse: <https://dataverse.scholarsportal.info/dataset.xhtml?persistentId=doi:10.5683/SP/J361HG>.

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