

SHORT COMMUNICATION

The apparently contradictory energetics of hopping and running: the counter-intuitive effect of constraints resolves the paradox

Anne K. Gutmann¹ and John E. A. Bertram^{2,*}**ABSTRACT**

Metabolic rate appears to increase with the rate of force application for running. Leg function during ground contact is similar in hopping and running, so one might expect that this relationship would hold for hopping as well. Surprisingly, metabolic rate appeared to decrease with increasing force rate for hopping. However, this paradox is the result of comparing different cross-sections of the metabolic cost landscapes for hopping and running. The apparent relationship between metabolic rate and force rate observed in treadmill running is likely not a fundamental characteristic of muscle physiology, but a result of runners responding to speed constraints, i.e. runners selecting step frequencies that minimize metabolic cost per distance for a series of treadmill-specified speeds. Evaluating hopping metabolic rate over a narrow range of hop frequencies similar to that selected by treadmill runners yields energy use trends similar to those of running.

KEY WORDS: Leg function, Muscle, Metabolic cost, Constrained optimization

INTRODUCTION

It is critical to our understanding of locomotion physiology and biomechanics to identify how energy is used by muscles to move the body. Kram and Taylor (1990) formulated a general cost function for running based on the hypothesis that ‘it is primarily the cost of supporting the animal’s weight and the time course of generating this force that determines the cost of running’. They assumed that during constant-velocity running, a substantial amount of mechanical energy could be stored and returned elastically by tendons so muscles would only need to do a small amount of work to lift and accelerate the body and limbs from stride to stride (Alexander, 1984; Ker et al., 1987). From this perspective, little metabolic energy would be used to perform mechanical work. Instead, most of the energy consumed would be used to activate muscles and develop the force needed to support body weight (Taylor, 1985; Roberts et al., 1997). Developing greater force or using faster fibers to develop a given amount of force more quickly would increase the amount of energy used (Rall, 1985; Heglund and Cavagna, 1987). Thus, Kram and Taylor (1990) predicted that ‘the rate of energy consumed by the muscles of a running animal per newton of body weight ($\dot{E}_{\text{metab}}/W_b$) is inversely proportional to the weight-specific rate of force application, W_b/t_c divided by W_b , where

t_c is the time for which the foot applies force to the ground during each stride...where c is a cost coefficient’, such that:

$$\dot{E}_{\text{metab}}/W_b = c \cdot 1/t_c. \quad (1)$$

One would expect that Kram and Taylor’s (1990) cost function (Eqn 1) would apply equally well to humans hopping in place as it should still be possible to store and return energy in tendons to reduce the cost of doing work, and there should still be the need to generate muscular force to support body weight. The muscles should also still need to contract at various rates in order to hop at a variety of frequencies. Surprisingly, we found that cost rate decreases with $1/t_c$ for vertical human hopping, which is opposite to the trend seen for human running. However, we present a resolution to this apparent paradox.

MATERIALS AND METHODS

For the first experiment, we measured oxygen consumption and ground reaction force for humans hopping in place on two legs over a range of frequencies. We set hop frequency by having subjects hop to the beat of a metronome. Subjects hopped for 4 min per frequency to allow enough time for oxygen consumption to reach steady state. Trials where subjects exceeded a respiratory exchange ratio of 1.0 were rejected. We calculated the rate of energy use by assuming that 20.1 J of energy were liberated for each milliliter of oxygen consumed. We calculated contact time based on ground reaction force data. This allowed us to plot metabolic rate as a function of contact time for hopping to test Kram and Taylor’s (1990) hypothesis in the context of hopping humans.

For the second experiment, we collected oxygen consumption and ground reaction force data for a variety of frequency–height combinations. We specified hop frequency by having subjects hop to the beat of a metronome as before, but we simultaneously specified hop height by getting subjects to adjust hop height using hop height feedback calculated from force plate output displayed on a computer monitor. This allowed us to force subjects away from their preferred hop height–frequency relationship so we could map the surrounding metabolic cost surface for vertical hopping in height–frequency space. We did not collect oxygen consumption and ground reaction force data for running, but instead used a cost surface previously generated from data available in the literature (Gutmann et al., 2006).

RESULTS AND DISCUSSION

In our first experiment, we found that rate of energy use for hopping decreased with the rate of force application, $1/t_c$ (Fig. 1A), opposite to the relationship observed for running (Fig. 1B) (Roberts et al., 1998). Such contradictory results might indicate that the cost of hopping is dictated by different mechanical and physiological factors from those that determine the cost of running, despite the fact that the two activities use a

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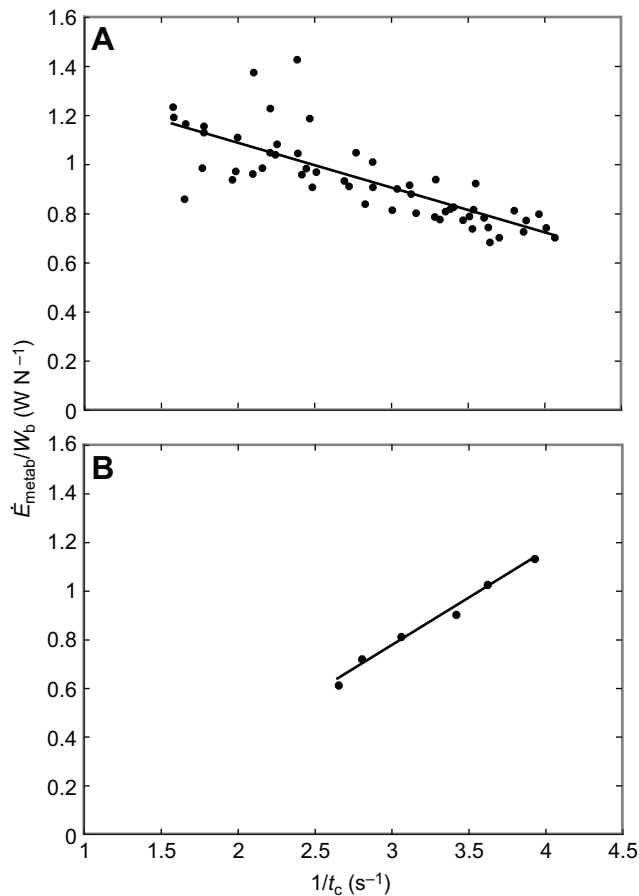


Fig. 1. Metabolic energy use rate trends appear to be opposite for hopping and running. (A) Hopping to the beat of a metronome. The weight-specific energy use rate, $\dot{E}_{\text{metab}}/W_b$, for people hopping in place to the beat of a metronome decreases with increasing rate of force application, $1/t_c$, where t_c is foot contact time. (B) Running on a treadmill. In contrast to hopping, the weight-specific energy use rate for people running on a treadmill reported by Roberts et al. (1998) increases with the rate of force application, $1/t_c$.

similar leg-determined bouncing motion. However, testing conditions can have a profound effect on subject response during locomotion. For instance, people choose a different speed–frequency relationship when walking on a treadmill versus walking to the beat of a metronome because energy use is minimized differently in the two circumstances (Bertram and Ruina, 2001; Bertram, 2005). Therefore, we decided to test whether the different energy use trends observed for hopping and running resulted from the conditions under which the data were collected, or were indicative of more fundamental differences between the mechanics and physiology of the two activities.

Humans and other animals generally choose gait parameters in a way that minimizes the energy used per distance traveled (Alexander, 1980, 1989; Hoyt and Taylor, 1981; Heglund and Cavagna, 1987; Usherwood and Bertram, 2003). In situations where individuals are completely free to select the values of all gait parameters (unconstrained conditions), they select values that globally minimize energy use. In situations where they are constrained to use a certain value of one gait parameter but are free to select the value of the remaining gait parameters (partially constrained conditions), they do the best they can and select the value that minimizes energy use to the extent allowed by the restrictions imposed (Bertram and Ruina, 2001; Bertram, 2005;

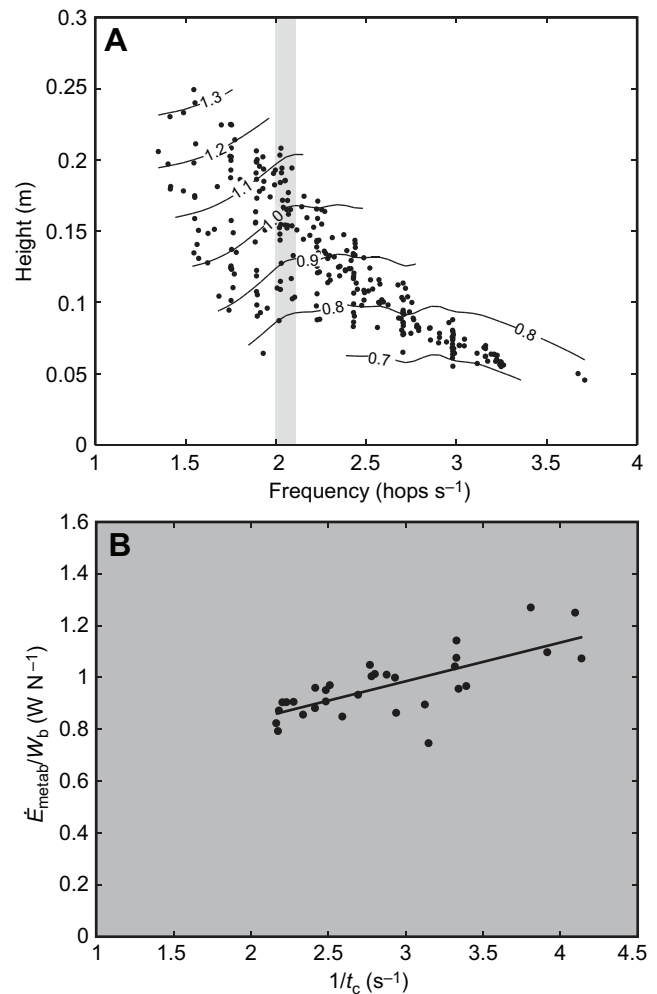


Fig. 2. Metabolic energy use rate increases with the rate of force application for hopping over a narrow range of frequencies. (A) We selected a narrow range of hopping frequencies (2.0–2.1 hops s⁻¹; gray band) from the hopping metabolic cost surface. This range of frequencies was similar (although not identical) to that naturally selected by people running under speed-constrained conditions on a treadmill. Contours of constant cost rate (W N⁻¹) are shown as thin black lines. (B) Plotting energy use rate as a function of rate of force application, $1/t_c$, for a narrow range of hopping frequencies (2.0–2.1 hops s⁻¹) yielded an energy use trend similar to that reported for running (Fig. 1B).

Gutmann et al., 2006; Gutmann and Bertram, 2013; Selinger et al., 2015). This can be conceptualized as minimizing energy use within a cross-section of a metabolic cost surface. Although an absolute minimum exists for the surface, it is not possible to attain this global minimum unless the constraint-determined cross-section happens to pass through the global minimum. The preferred gait parameter relationship for a given constraint condition results from optimizing energy within a series of cross-sections, each corresponding to a different constraint value. An example of this would be measuring self-selected step frequencies across a series of treadmill speeds to build a preferred speed–frequency relationship. The optimal gait parameter relationship and, hence, the optimal metabolic energy use relationship observed will depend on the shape of the metabolic cost surface and the orientation of the constraint cross-sections. The shape of the metabolic cost surface is in turn determined by the relationship between metabolic energy use and muscle mechanics, and the orientation of the constraint cross-sections is determined by

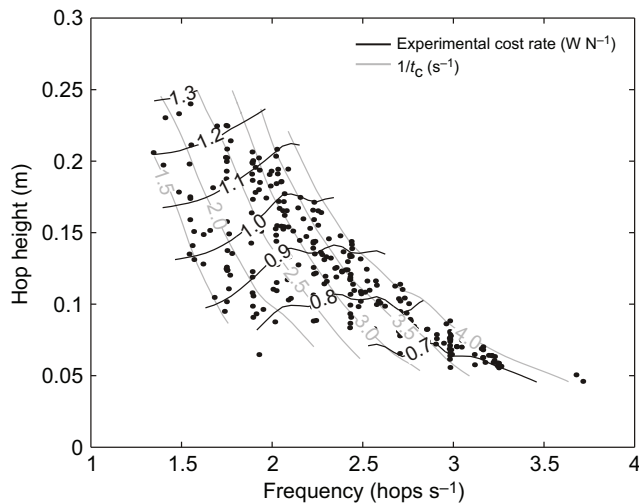


Fig. 3. Metabolic energy use rate for hopping compared with rate of force application, $1/t_c$, across a wide range of height–frequency combinations. In general, $1/t_c$ (gray) does not do a good job of predicting metabolic energy use rate for human hopping. Empirical cost contours (black) are determined from the data points indicated. The two sets of cost contours are nearly perpendicular across most of the height–frequency combinations studied, indicating that the shape of the experimental metabolic cost rate surface for hopping differs substantially from the shape of the metabolic cost rate surface predicted by Kram and Taylor's (1990) cost function (Eqn 1).

which gait parameters are constrained and which are freely selected by subjects.

In our first hopping experiment, subjects were required to hop using a wide range of frequencies specified by a metronome but were free to select hop height (frequency-constrained conditions). By contrast, in running studies, subjects were required to run using a wide range of speeds specified by a treadmill (Roberts et al., 1998) but were free to select step frequency (speed-constrained conditions). Because of the shape of the metabolic cost surface for running, subjects naturally selected a relatively narrow range of step frequencies (2.6–3 steps s^{-1}) in order to minimize the energetic cost per distance traveled for each speed (Gutmann et al., 2006). As a result, we originally compared two very different cross-sections of each cost surface – a cross-section that spanned a wide range of frequencies for hopping (Fig. 1A) and a cross-section that spanned a narrow range of frequencies for running (Fig. 1B). To make a more valid comparison, we selected a narrow range of frequencies for hopping, similar to the range selected via energy optimization under speed-constrained conditions for running (Fig. 2A) and then compared metabolic rate versus rate of force application for hopping and running. In this case, the metabolic rate for hopping increased linearly with the rate of force application just as it had for treadmill running (Fig. 2B). This suggests that the same mechanical and physiological features determine the cost of hopping and running, and that the original differences observed were due to differences in observational perspective created by different constraints rather than fundamental differences between the mechanics and physiology of the two activities.

Kram and Taylor's (1990) force rate cost function (Eqn 1) has been successfully used to predict the relationship between gait parameters and metabolic cost for various kinds of locomotion (Weibel et al., 1992; Kram and Dawson, 1998; Kram, 2000; Saibene and Minetti, 2003; Sih and Stuhmiller, 2003). This function does a good job of predicting metabolic energy use rate over a fairly narrow range of frequencies – both when the

frequencies are naturally selected in response to a constraint (as happens in speed-constrained treadmill running studies) and when the frequencies are artificially selected after the fact (as we did in the current hopping study; Fig. 2B). However, this function is not adequate for predicting metabolic energy use rate under other conditions (Fig. 3) – namely the broad range of frequencies we required subjects to use during frequency-constrained hopping. As such, the force rate cost function appears to be a special case of a more general cost function that more thoroughly represents the constitutive features of muscle function during bouncing gaits. Such a general cost function might be based on the metabolic cost per time of activating a given muscle volume to support body weight for the duration of ground contact (Pontzer, 2007) and the metabolic cost per time of swinging the legs. Metabolic cost per hop of human hopping appears to increase with muscle impulse of the knee, which suggests that metabolic cost per time depends on both the muscle volume recruited to produce a given force and the fraction of the hop when the muscle is active, i.e. duty factor (A.K.G. and J.E.A.B., unpublished data). Additionally, both metabolic cost per time and active muscle volume increase with forward velocity for running (Biewener et al., 2004) and the cost of leg swinging appears to account for a nearly constant fraction of metabolic cost per time (Doke et al., 2005), suggesting that the metabolic cost of running may depend on the cost of activating a given muscle volume during ground contact as well. These findings highlight the importance of understanding how testing conditions affect the apparent relationship between mechanical variables and metabolic cost, and the need to find a general cost function for bouncing gaits that accurately describes the complete relationship between the mechanics and metabolic cost of these gaits across a wide range of conditions.

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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 analyzed hopping data and analyzed running data extracted from the literature. 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 have been deposited in Dataverse at <https://dataverse.scholarsportal.info/dataset.xhtml?persistentId=doi:10.5683/SP/XLINXQ>

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