Reconsidering the Effects of Respiratory Constraints on the Optimal Running Speed

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ABSTRACT

WILLCOCKSON, M. A., and C. M. WALL-SCHEFFLER. Reconsidering the Effects of Respiratory Constraints on the Optimal Running Speed. Med. Sci. Sports Exerc., Vol. 44, No. 7, pp. 1344–1350, 2012. Introduction: Although both humans and quadrupeds frequently coordinate breathing and limb movement during running, early studies in humans focused on how increased breathing flexibility in humans allowed for relaxed or even transient coordination during locomotion. This difference was used to explain why quadrupeds had an optimal running speed whereas humans did not. Recent research, however, has clearly demonstrated that humans, like quadrupeds, have an optimal running speed. Because these findings are new, it remains unclear why this is true: whether because entrainment in humans was more important than initially predicted or because another restraint is acting. Here, we try to explain the observed minimum cost of transport (CoT) by analyzing metabolic cost with respect to entrainment and a standard set of anthropometrics. Methods: We measured the energetic cost of human running at five different speeds and calculated individual CoT curves for each participant (N = 9). Simultaneously, entrainment was determined by the degree to which a poststimulus histogram (breaths per 0.05-s bin after a footfall) differed from a uniform plot. Results: We compared the degree of entrainment to each participant’s optimal running speed and found that although all of our subjects clearly entrained at some speeds, entrainment was not a function of CoT (P = 0.897). Because entrainment was also not correlated with speed (P = 0.304), it seems that bipedalism removed the respiratory constraints associated with quadrupedalism as originally suggested. Conclusions: Unlike quadrupeds, for whom respiratory constraints remain implicated in the speed dependence of CoT, constraints that lead to a minimum CoT for people must involve other mechanisms of efficiency such as the storage and release of energy in the lower limbs. Key Words: ENTRAINMENT, ENERGETICS, LOWER LIMB LENGTH, COST OF TRANSPORT

EARLY EXPERIMENTATION

In humans, the relationship between the energetics of running and running mechanics has been challenging to understand, particularly because this relationship pertains to the advantages of bipedalism over other forms of locomotion like quadrupedalism. Because locomotor–respiratory coupling (i.e., entrainment) has been heavily implicated in the curvilinear cost of transport (CoT) in quadrupeds (5), the observation that humans were not subject to the same strict breathing parameters as quadrupeds was intuitively expanded to explain the flat CoT described in early experimentation with people (21). Carrier (7) characterized the factors that constrain horses to run at an optimal running speed in the following manner:

For sustained economical transport a running mammal must therefore (1) employ an energetically appropriate blend of stride length and stride frequency, (2) match the metabolic demand for oxygen via lung ventilation, (3) ventilate the lungs with an energetically suitable combination of breath frequency and volume, and (4) breathe in synchrony with the locomotor motions of the body.

In this way, entrainment in quadrupeds—which occurs because of the direct impact and subsequent compression of the thoracic cavity during proximal limb loading—results in only a narrow range of speeds within a gait for which respiration and gait tuning can be optimized.

Respiratory flexibility provided a key piece to the cohesive theory for understanding how the mechanics of bipedalism affected energetic costs (7). Because bipeds do not experience compression due to proximal limb loading, they were initially deemed free of respiratory constraints, and this flexibility was a major piece in the long-held hypothesis that people in particular did not have a curvilinear relationship between speed and the CoT (7). Furthermore, humans have been observed to use more than five different coupling ratios (4:1, 3:1, 2:1, 1:1, 5:2, and 3:2) (5) and entrain either
DISCOVERY OF OPTIMAL RUNNING SPEEDS IN HUMANS

Now, with new experimental evidence of an optimal running speed in humans (27), it is unclear what role, if any, entrainment may have in modulating cost. Has the role of breathing flexibility in humans been exaggerated? Or perhaps, does the suggested plasticity in locomotor–respiratory coupling exist but not contribute to whole-organism energetics in a predictable way (30)? Although other tuning mechanisms such as muscular recruitment, tendon loading, or lower limb–spring function (e.g., the spring–mass model) (6,14) are all possible factors contributing to the energetic cost of human running, the primary purpose here is to re-evaluate Carrier’s initial hypothesis to determine whether entrainment in humans can explain a substantial part of the variation observed in CoT. Although entrainment has been examined at length in humans with respect to key variables such as mass, experience, speed, load, and metabolic cost (3), this is the first study that attempts to relate the phenomenon of entrainment to the newly documented landmark: optimal running speed.

HYPOTHESES TESTED HERE

If entrainment constrains energy consumption, we predict that runners will entrain maximally near the optimal running speed. Although humans have been shown to maintain entrainment in a variety of manners as summarized previously (5), entrainment may still systematically shape the CoT curve in running. Our hypothesis stems from the same reasoning used to explain CoT in quadrupeds: 1) the optimal running speed occurs when the natural frequencies of limb movement and breathing most closely match; 2) above and below the optimal running speed, the natural frequencies of the limbs and respiratory system become increasingly different, and the advantages presented by reduced antagonistic muscle contraction are offset by ineffective breathing frequencies; and 3) when the detriment of breathing restrictions become too large, a shift occurs so that a new breathing frequency is adopted (7). At the energetically optimal speed, we expect the natural frequencies of breathing and limb movement to be well matched in the most commonly observed 2:1 ratio. Above and below this speed, we expect runners will begin to entrain sporadically or with different ratios to accommodate the increasingly disparate natural frequencies of breathing and limb movement. We test these predictions by determining each runner’s optimal running speed with careful replicates. At the same time, we collected breathing and stride data to detect entrainment using a poststimulus histogram. We also measured each runner’s standard anthropometrics to determine whether body size or shape has significant predictive power on the optimal running speed.

METHODS

Subjects. The protocol was approved by Seattle Pacific University’s Institutional Research Board, and all participants signed written informed consent. We measured each subject’s stature, mass, bi-iliac breadth, and lower limb length (LLL). Stature and mass were measured at the same time using a stadiometer; participants were shoeless and wore shorts and a T-shirt during the measures. Participants ran with their shoes on. LLL was measured as the linear distance from the greater trochanter to the lateral malleolus (26). Mean anthropometrics are listed in Table 1. Each participant recorded the number of minutes they aerobically exercised each week as a metric for experience. Although the athletic backgrounds of our participants were intentionally varied (i.e., college soccer, college track, recreational marathoners, casual runners) to prevent against a conditioning effect associated with a single sport, there were two fitness requirements: 1) participants must exercise at least three times a week aerobically for >60 min each time and 2) participants had to be able to perform the whole protocol without exceeding a respiratory quotient of one (the anaerobic threshold). The protocol consisted of nine experimentally naïve participants (six women and three men, mean age = 20.7 yr).

We assessed the power of this study using reference tables relating sample size, power, significance criterion, and effect size (see Reference 10, page 567). Using an α of 0.05 for the significance level, our sample size of nine gave us 82% power to detect correlations of the size deemed relevant for our purposes (r ≥0.8).

Equipment. Subjects ran on a motor-driven treadmill that was calibrated by measuring the length of the belt and then recording the time for 10 revolutions at every 0.2-ms⁻¹ interval from 0.9 to 4.5 ms⁻¹. Metabolic rate was monitored using an Oxycon mobile portable ergospirometer (CareFusion), which reported a breath-by-breath analysis of oxygen consumed and carbon dioxide produced (L·min⁻¹). Breathing frequency was measured at 100 Hz using a small thermosensor (Vernier) that was fitted inside the air vent of the mask (19,29). Each breath was broken into an exhalation, the first abrupt increase in temperature, and inhalation, the first abrupt decrease in temperature. Stride frequency

<table>
<thead>
<tr>
<th>Anthropometrics</th>
<th>Mean ± SD</th>
<th>Males (n = 3)</th>
<th>Females (n = 6)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass (kg)</td>
<td>74.4 ± 5.3</td>
<td>59.8 ± 4.9</td>
<td></td>
</tr>
<tr>
<td>Stature (cm)</td>
<td>179.5 ± 7.3</td>
<td>167.6 ± 3.6</td>
<td></td>
</tr>
<tr>
<td>LLL (mm)</td>
<td>885.0 ± 20.6</td>
<td>848.5 ± 33.8</td>
<td></td>
</tr>
<tr>
<td>Bi-iliac breadth (mm)</td>
<td>252.7 ± 24.4</td>
<td>234.2 ± 13.3</td>
<td></td>
</tr>
<tr>
<td>Optimal speed (ms⁻¹)</td>
<td>3.83 ± 0.30</td>
<td>3.16 ± 0.39</td>
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Males were larger than females in all measures, although this reached significance only for mass (P = 0.018). Males also had significantly faster optimal running speeds (P = 0.038).
was recorded with a sound level meter (Vernier) at 100 Hz, which captured the sound of each impact with the treadmill (5). The beginning (and middle) of each stride was defined by the first abrupt increase in the sound meter indicating foot strike.

Although a consistent lag in either the thermosensor or sound meter would not pose a problem in identifying entrainment (because a poststimulus histogram compares the relative position of each signal), significant variation in the lag of either device would be problematic. To validate that our equipment was suitably sensitive, we had both instruments record the same stimulus 10 times (an impulse of loud, hot air) to ensure that the variation in reporting time was consistently ±0.01 s (SD).

Running trials. We simultaneously measured metabolic cost and the entrainment of breathing to limb movement during running at each of five different speeds. Each speed was maintained for 5 min. Participants were instructed to pick five aerobically manageable speeds (respiratory quotient (RQ) < 1) from a series of options: two speeds they considered slow (1.79, 2.26, or 2.73 ms⁻¹), two speeds they considered medium (2.73, 3.15, or 3.63 ms⁻¹), and one speed they considered to be fast (3.15, 3.63, 4.04, or 4.51 ms⁻¹). Between each bout of running, participants were instructed to walk slowly until their metabolic rate returned to walking values. Participants ran at all five speeds in a different randomized order on at least three separate days within a 2-wk period; each collection was at least 48 h apart.

Data analysis. VO₂ and RQ values were converted to kilocalories and watts using Weir’s (32) standard calculation. Metabolic values were averaged to get the final cost of locomotion (cost per unit time) for individuals at a given speed. From these data, we calculated CoT in joules per kilometer. CoT minima were calculated by fitting a polynomial curve to the data and solving for the minimum (27).

The entrainment of breaths to footfalls was determined using a cross-correlation of the two events. Like a poststimulus histogram, each impact of the foot (stimulus) with the ground began a 256-bin sequence; each bin was 50 ms wide (2). Every time an exhalation began, one count was added to the bin at the corresponding time, such that entrainment would result in the accumulation of points in several nearby bins, whereas no entrainment—i.e., no association between the signals—resulted in a random distribution of breaths throughout all bins (Fig. 1).

Although one of the most common metrics to quantify a poststimulus histogram is to define entrainment as the percent of breaths that occur within 0.05 s of the stimulus (%E) (3), we have modified the metric slightly because we believe that, although %E is intuitive, it is prone to artifacts. Artifacts arise because as speed increases (and, to a lesser extent, stride frequency), the 0.05-s window used to denote breaths “near footfall” becomes an incrementally larger proportion of each stride. In an exaggerated scenario, a runner with a stride length of 1.5 m per stride running 30 mph (0.05s per stride) would result in a %E of 100% regardless of whether stride and breathing were coupled at all.

As an alternative, we calculated the “entrainment coefficient” (EC) given by the following equation: (actual number of breaths − number of breaths predicted by random chance) / number of breaths predicted by random chance. By comparing the observed histogram with the number of footfalls expected by random chance and not a fixed time interval, a gradual increase in EC with speed was prevented. Using this method, an EC of 2 (where, for example, five breaths were expected by chance) denotes an interval where 10 breaths (200%) were observed in a bin above that predicted by chance (similar to Paterson et al. [22]).

Statistics. To assess our hypothesis regarding the relationship between EC and CoT, we tested whether there was a statistically significant negative correlation. Such a relationship would suggest that the coupling results in lower costs. Statistical analysis consisted of bivariate correlations and linear regressions; all analyses were done using SPSS 18.0 (PASW Statistics).

RESULTS

Metabolic cost and entrainment. Metabolic data from each participant were well described using a curvilinear fit as in Steudel-Numbers and Wall-Scheffler (27) (mean R² = 0.9043; Fig. 2); mean optimal speeds are listed in Table 1. When we compared each runner’s CoT with entrainment, entrainment did not significantly explain the variation in cost for any individual, using either a curvilinear or
a linear fit ($P > 0.1$) (Fig. 3). In addition, a $t$-test comparing EC at the optimal running speed and speeds away from the optimum showed no significant differences ($P > 0.2$).

Although entrainment was not predicted by speed ($P = 0.304$), stride length ($P = 0.165$), experience ($P = 0.08$, $r = -0.608$), or cost ($P = 0.098$), we consistently observed some degree of entrainment in all of our participants (0.5188 EC ± 0.3743; Fig. 1B). As speed independence would predict, the SD of EC was as great when trials were grouped by day (five speeds of a specific trial) or by speed (three to five runs at the same speed on different days).

**Metabolic cost and anthropometrics.** To better understand the relationship between anthropometrics and the optimal running speed, we combined the results from the present study with those from Steudel-Numbers and Wall-Scheffler (27) (total $N = 18$) and tested for anthropometric predictions. All anthropometrics were entered into a model predicting the speed of the minimum CoT in a stepwise fashion; LLL was the strongest predictor of the speed at which the minimum CoT occurred ($P = 0.004$, $\beta = 0.637$, $R^2 = 0.406$) (Fig. 4).

**DISCUSSION**

The primary purpose of this experiment was to reexamine the hypothesis of a functional relationship between entrainment and energetic optimality in human running (7), specifically, whether humans have an “optimal” breathing pattern that corresponds with their energetically optimal speed. Second, we introduced a new metric, the EC, to quantify the level of entrainment of an individual for a given trial. Finally, we tested possible relationships between the optimal running speed and morphology by combining our data.
with the original article identifying an optimal running speed in humans.

**Entrainment during running.** Previous studies have not been able to find convincing evidence of universal trends in entrainment with respect to running conditions. It is possible, however, that an underlying relationship between entrainment and CoT may have been obscured because, until recently (27), the curvilinear relationship between running speed and metabolic cost was not appreciated. This, combined with the understanding that entrainment is a widely accepted explanation for the CoT curve in quadrupeds (1,5), made the result that entrainment in humans was not implicated in the CoT ($P = 0.565$) surprising (Fig. 3). Nevertheless, we are confident in our results because a post-stimulus histogram—as used here and in previous studies (2,16)—provides a rigorous way to detect entrainment that is particularly resilient to false findings, such as the false positives and negatives that can arise using the integer ratio of strides to breaths (4) or coincidence of onset (3), respectively.

Now that it is clear that the model for the mechanics and energetics of running in quadrupeds as it relates to entrainment constraints cannot be applied to humans, we must ask two new questions: if bipedalism removed the respiratory constraints that are implicated in sculpting the CoT in quadrupeds, 1) why do humans still widely entrain breathing to limb movement, and 2) if entrainment does not predict cost, what tuning mechanisms account for the CoT curve in humans?

The seemingly vestigial behavior of entrainment in humans was addressed briefly by Bramble and Carrier (5), who suggested that experienced runners entrain regularly, whereas amateur runners do not. This trend, however, did not hold true in our own sample ($r = -0.608$), and other studies have frequently observed entrainment in nonhabitual runners (3,12). Perhaps the simplest explanation for the persistence of entrainment in humans is that the impact of the distal limbs with the ground triggers enough of an impulse in the thoracic cavity to bias breathing but in a more subtle way than in quadrupeds, too subtly to shape the cost of running visibly (12). This notion seems reasonable because it relies on the same explanation used in quadrupeds and has been further supported by research on human breathing patterns in wheelchairs and during arm-specific exercises (12). Although entrainment is not a simple relationship between mass (force) and entrainment (mass and entrainment are not correlated ($P = 0.297$)), the involvement of active muscles and the movement of the abdominal viscera all support the notion of some biomechanical involvement in the entrainment that occurs during human running (12). In addition, work on the pattern of (respiratory) abdominal muscle activity during treadmill running suggests abdominal muscles may actually be recruited as “accessory locomotor muscles,” and as such, their recruitment will consistently be correlated with both breathing and running activity (12(p465),13); however, because breathing is still a “neurally mediated event,” the development of any suggestive locomotor–respiratory interactions has been shown to remain independent of rigid entrainment (12(p472–3),13).

**Biomechanical alternatives for the running speed optimum.** With the exception of early data collected on human running (20,21), now falsified (27), there are no known examples of cost invariant transport in quadrupeds or bipeds. Because both bipedal walking and running have now been shown to have optima, it is no longer possible to argue that relaxation of respiratory constraints in bipeds determines the CoT curve. Rather, we see that the energetic cost of bipedal locomotion is necessarily dependent on speed as with other terrestrial vertebrates (15). Intuitively, this is reasonable because locomotion involves a multisystem balance of speed-dependent systems, e.g., cardio, respiratory,

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**FIGURE 3**—The EC does not vary predictably as a function of CoT ($P > 0.1$ for each individual). Each shape and shading represents a different individual.

**FIGURE 4**—Significant linear relationship between LLL and the speed at which the minimum CoT occurs ($P = 0.004, \beta = 0.637, R^2 = 0.406$). This relationship indicates a close correlation between limb length and optimal running speed; any causal link between these two variables should be the focus of future investigations into running economy and morphological variations.
skeletal–muscular, and thermoregulatory (6,7,9). Although it remains unclear what tuning causes the running optimum in humans, it is likely that numerous biomechanical factors are involved.

For example, lower limb movement in running humans is well modeled using a spring–mass model where the lower limb functions as a spring with variable stiffness (14). As the runner falls in the middle and end of the stride, her vertical movement slows, and the kinetic energy is stored in the lower limb as potential energy until it is released as the runner rises again. How the efficiency of this process changes with respect to speed and cost has not been fully described and may provide some insight into the determination of the optimal speed. Early data on the change in effective LLL during the stance phase of running—modeling lower limb compression—supports the theory of efficient storage and release of energy at the optimal running speed (C.M.Wall-Scheffler, unpublished data, 2012). Data on the average muscle activity of the lower limb muscles augment this approach: because the muscles account for much of the cost of locomotion, some optimal level of muscular activity may be the dominant factor determining the cost of running as different muscles become more (or less) engaged. New research using integrated EMG suggests that, in fact, there is reduced muscular activity throughout lower limb muscles around the optimal speeds of both running and walking (Fig. 1 of Carrier et al. [8]).

Optimality of human running: anthropometrics.

Finally, the effect of LLL on locomotor efficiency has been the subject of significant discussion. Although early studies, which looked across species, did not demonstrate a relationship between LLL and locomotor efficiency (23–25), recent data sets investigating within-species variation has served that the CoT curve shifted to higher speeds as LLL increased. As a result, longer LLL causes the optimal running speed to increase. Future research should evaluate whether this trend persists with a larger sample size and the nature of this relationship (what might be driving this correlation). Also, more importantly, because selection pressures in humans likely centered on walking, not running, further research is required to see if a similar phenomenon is true for the CoT during walking (18,31).

CONCLUSIONS

Obtained results have implications for our understanding of locomotor economy. Because it has been suggested that elite distance running performances are driven by increased metabolic economy or efficiency (11), we expect people with faster optimal speeds to win races. Because our work has illuminated morphological relationships between fast optimal speeds (e.g., long LLL), this further suggests a specific morphological advantage.

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