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Walking, running, and resting under time, distance, and average speed constraints: optimality of walk–run–rest mixtures

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On a treadmill, humans switch from walking to running beyond a characteristic transition speed. Here, we study human choice between walking and running in a more ecological (non-treadmill) setting. We asked subjects to travel a given distance overground in a given allowed time duration. During this task, the subjects carried, and could look at, a stopwatch that counted down to zero. As expected, if the total time available were large, humans walk the whole distance. If the time available were small, humans mostly run. For an intermediate total time, humans often use a mixture of walking at a slow speed and running at a higher speed. With analytical and computational optimization, we show that using a walk–run mixture at intermediate speeds and a walk–rest mixture at the lowest average speeds is predicted by metabolic energy minimization, even with costs for transients—a consequence of non-convex energy curves. Thus, sometimes, steady locomotion may not be energy optimal, and not preferred, even in the absence of fatigue. Assuming similar non-convex energy curves, we conjecture that similar walk–run mixtures may be energetically beneficial to children following a parent and animals on long leashes. Humans and other animals might also benefit energetically from alternating between moving forward and standing still on a slow and sufficiently long treadmill.

1. Introduction

Imagine you wish to go from your house to the bus stop and have very little time to do so. You would likely run the whole distance. If you had a lot of time, you would likely walk the whole distance. If there was an intermediate amount of time, perhaps you would walk for a while and run for a while. While it is not immediately obvious that using a walk–run mixture is advantageous here, it seems consistent with common experience. In this article, we make this anecdotal experience precise by performing human subject experiments. Most significantly, we then interpret the experimental observations using metabolic energy minimization, without appealing to fatigue or poor time-estimation as mechanisms. We review and extend various mathematical results related to metabolic energy minimization and locomotor choice, deriving, for the first time, predictions for travelling finite distances and for travelling on treadmills of finite lengths, in the presence of costs for the transients, using analytical arguments and numerical optimization. In these models, the key mathematical criterion for obtaining walk–run (and walk–rest) mixtures is non-convexity of the energy cost curves. Assuming similar energy curves, we conjecture that similar walk–run–rest mixture strategies may be energetically beneficial in superficially diverse situations: children walking with parents, animals on long leashes or long slow treadmills, non-elite marathon runners, etc.

2. An overground gait transition experiment

2.1. Background

Humans have two qualitatively distinct ‘gaits’, walking and running. Some *treadmill gait transition experiments* have shown that a person walking on a slow

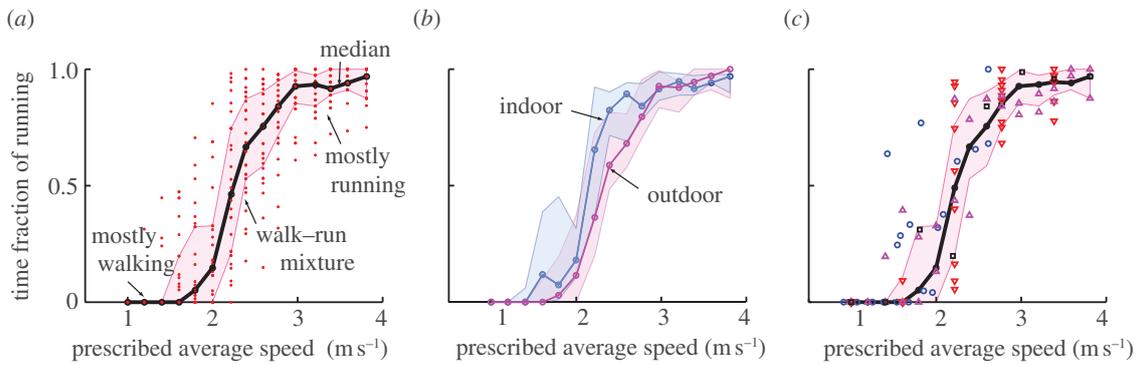


Figure 1. (a) All subjects with the basic protocol ($n=28$ subjects, indoor and outdoor, $D_{\text{required}}=122$ m). The time fraction of running is shown: the red dots are the raw data (each dot is a trial, all data points shown), the solid black line is the population median, and the pink band denotes 50% of the data centred around the median (25th–75th percentile). Pure walking dominates low prescribed speeds and pure running dominates high prescribed speeds, and most subjects use a walk–run mixture for intermediate speeds. (b) The data in the previous panel, decomposed into indoor and outdoor data. Median fractions are blue and pink solid lines, surrounded by the respective 50% bands in corresponding lighter shades. (c) Variants of the basic protocol overlaid on the 50% band from the first panel: experiments in which subjects had three trials per prescribed average speed for five different prescribed average speeds (red triangles), in which the trials had different random distances ranging between 70 and 250 m and different time allowed (blue circles), in which the subject travelled twice the distance, 244 m (black squares), and in which the subjects were allowed to arrive earlier than T_{allowed} (magenta triangles).

treadmill switches to running when the treadmill speed is slowly increased [1–3]. When the speed is decreased, the person switches from running to walking. Historically, most such gait transition experiments have been performed on a treadmill. Because an ideal treadmill (with perfect speed regulation) is an inertial frame, treadmill locomotion has the potential to be mechanically identical to overground locomotion [4]. However, treadmill locomotion is different from overground locomotion in two key respects. First, a treadmill with a short length limits voluntary speed fluctuations by the subject. No such strict speed constraint exists in real life. Second, a typical treadmill provides no visual flow, the feeling of objects moving past one’s eye (but see [5]). Thus, in part to make these experiments more ecological, we introduce a simple non-treadmill *overground gait transition experiment*.

2.2. Experimental protocol

In the ‘basic protocol’ of our experiment, the subjects had to go from a starting point S to an endpoint E, separated by a distance D_{required} , in a given time duration T_{allowed} . The subjects carried a stopwatch that counted down to zero from the total time duration T_{allowed} , so they could see, when necessary, the time remaining. The subjects had to reach the endpoint exactly when the stopwatch ran out, rather than arrive early or late. The subjects received no further instructions.

By constraining the total distance and the total time, we are prescribing an *average speed constraint* $V_{\text{avg}} = D_{\text{required}}/T_{\text{allowed}}$, without constraining the speed at any moment. Each subject had 15 trials, with different T_{allowed} resulting in prescribed average speeds V_{avg} from 1 to 3.8 m s^{-1} . All subjects were video-taped and instrumented for stride frequency. Some subjects were instrumented with a global positioning system (GPS) device for speed measurements. Some subjects performed indoor trials, and others, outdoors.

Variants of this ‘basic protocol’ were performed for small subject numbers, using longer and different distances, allowing some trial repetition, and allowing arriving early, to check if the results change substantially with protocol details. See §7 at the end of this article and electronic supplementary material, §S5 for more details.

2.3. Experimental results: walking and running fractions

The subjects were able to travel the distance on time, with the mean and standard deviations of late arrival just over a second. If the subjects approached the destination too early, they slowed down to arrive on time. As expected, for low prescribed average speed V_{avg} , the subjects walked the entire distance. For high V_{avg} , the subjects ran almost the entire distance. For intermediate V_{avg} , a majority of the subjects used a mixture of walking and running (a walk–run mixture).

Figure 1a shows the fraction of running as a function of the prescribed average speed V_{avg} for all the subjects involved in the basic protocol. A single data point (red dot) in figure 1a is the fraction of time spent running by one subject in one trial, obtained from the video by counting the seconds spent running; also shown are the median running fraction as a function of average speed and a (pink) band containing 50 per cent of the data points. Here, running is defined as any gait with a flight phase, in which the hip goes down and then up when one leg is in contact with the ground, as if the body bounces on a springy leg [6]. In walking, the hip vaults over on the leg more like an inverted pendulum and at least one foot always contacts the ground [7].

Unlike on a treadmill, there is no sharp gait transition speed here. Instead, there is a ‘transition region’ between average speeds of 2 and 3 m s^{-1} (roughly), in which a majority of the subjects use a walk–run mixture, transitioning from walking most of the time to running most of the time. The average speed with equal amounts of walking and running (running fraction = 0.5) is about 2.2 m s^{-1} in figure 1a, which is close to, but slightly higher than the treadmill gait transition speeds in the literature [1,3]. At the highest average speeds, the running fraction is not quite 100 per cent, but this might be because the subjects walked one or two steps before running the rest of the way; longer D_{required} may find higher running fractions.

The indoor and outdoor trials (figure 1b), while yielding qualitatively similar trends appear to be slightly different; outdoor data’s median is close to the indoor data’s 25th percentile. These differences could be due to small differences in protocol (having to turn around indoors), and increased visual flow indoors due to nearby walls, resulting in higher

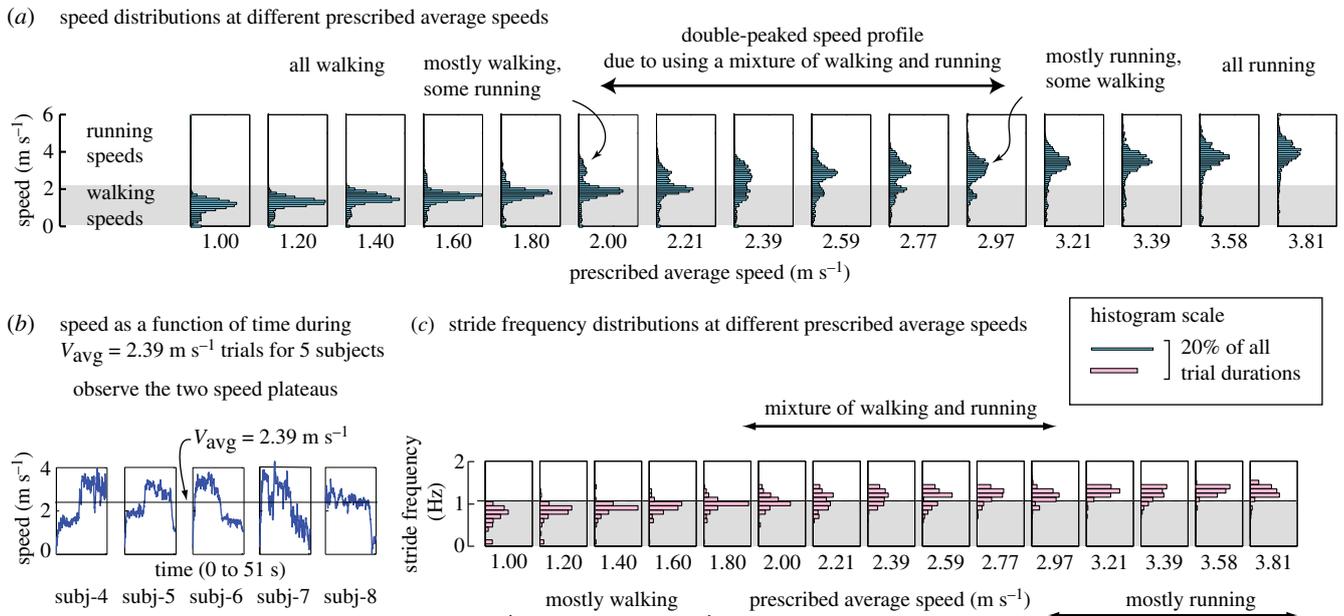


Figure 2. (a) Histograms of the speeds at which the subjects travelled during each of the 15 trials with different prescribed average speeds V_{avg} ; pooled over the 10 subjects with GPS speed measurements, with histogram bin width = 0.1 m s^{-1} . The histograms have a single peak for low and high prescribed average speed, but have two peaks for intermediate average speeds, suggesting a walk–run mixture. (b) The unfiltered GPS-derived speed as a function of time during the trial corresponding to $V_{\text{avg}} = 2.39 \text{ m s}^{-1}$ and $T_{\text{allowed}} = 51 \text{ s}$, for five subjects. Notice the two speed plateaus in subjects 4–6. (c) Histograms of stride frequencies used during various trials, pooled over outdoor subjects with this pedometer-based data. Histogram bin width = 0.1 Hz . The horizontal scale of the histograms are such that the area within the histogram are the same across different prescribed speeds (proportional to total number of trials). The horizontal grey band across the histograms (a and c) indicating normal walking and running speeds or frequencies is simply to guide the eye, not meant to be a strict separator.

perceived speed, shifting the actual gait transition region to lower speeds [5,8]. The data from the protocol variants, taken as a whole, are not qualitatively different from the basic protocol (figure 1c); 75 per cent of the protocol variants' data points fell within the centred 50 per cent band of the data from the basic protocol.

2.4. Experimental results: speed variations within a trial

When the subjects used a walk–run mixture, the walking speed was low and the running speed was high, so that the average speed is as prescribed. Figure 2a shows the trial-by-trial distribution of speeds pooled over all the outdoor subjects with GPS speed measurements. As we would expect, with increasing prescribed average speed, the speed distribution slowly shifts upward to higher speeds.

Significantly, the speed distribution is double-peaked for V_{avg} between 2.0 and 3 m s^{-1} . Such double-peaked distributions indicate (many) subjects walking slow and running fast in a walk–run mixture. At $V_{\text{avg}} = 2 \text{ m s}^{-1}$, the lower speed walking peak has a higher enclosed area (in the histogram) than the higher speed running peak, suggesting that subjects walked for most of the time. The relative sizes of the peaks are reversed at $V_{\text{avg}} = 2.97 \text{ m s}^{-1}$, when subjects ran most of the time. For V_{avg} below 2 m s^{-1} and above 3 m s^{-1} , we observe only a single peak in the speed distributions, indicative of walking or running the whole distance.

Figure 2b shows the raw GPS-derived speed as a function of time for five subjects, for the $V_{\text{avg}} = 2.39 \text{ m s}^{-1}$ trial, which is in the walk–run transition region. For three subjects shown (subjects 4–6), we see two distinct speed plateaus, corresponding to running and walking. Not all subjects had such distinct speed plateaus in the transition regime. To illustrate subject-to-subject variability (also seen in figure 1), we

show one subject (subject 7) for whom the plateaus are less distinct, and another subject (subject 8) who used roughly the same speed over the whole trial.

The stride frequency histograms shown in figure 2c also show a speed region (about $2\text{--}3 \text{ m s}^{-1}$) in which the stride frequency distribution is broader, overlapping both walking and running stride frequencies. In this region, however, the histograms are not as distinctly double-peaked, perhaps both on account of larger subject-to-subject variability and higher measurement errors in the stride frequencies (see the electronic supplementary material).

3. Energy minimization as a candidate theory of gait choice

3.1. On a treadmill, switch to save energy

Margaria [2] and others found that walking requires less energy at low speeds and running requires less energy at higher speeds, as also suggested by mathematical models of bipedal walking and running [7,9–11]. Example walking and running metabolic rates as functions of speed, based on published data [12–15], are shown in figure 3a. On a treadmill, humans switch between walking and running close to the intersection of the cost curves (Q). While some researchers [1,16,17] found a small difference ($\sim 0.1 \text{ m s}^{-1}$) between the energy-optimal and measured treadmill transition speeds (and also a slight difference between the walk-to-run and run-to-walk transition speeds [1]), others [18,19] did not; see [9,20] for possible explanations.

We now describe what metabolic energy minimization predicts in the context of our non-treadmill experiment, first

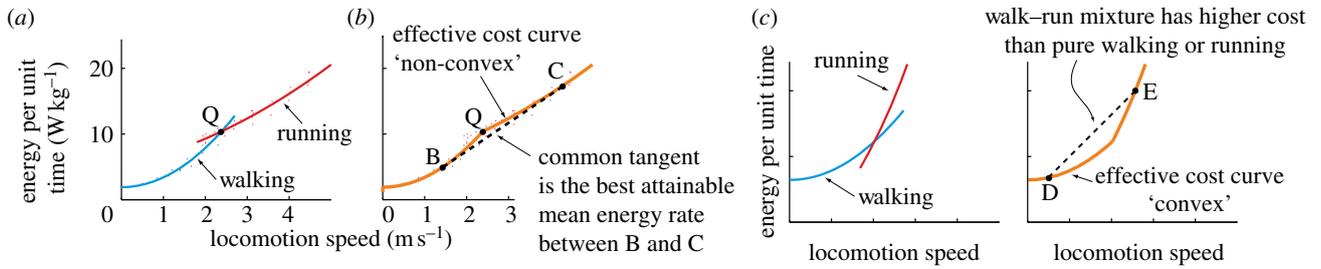


Figure 3. (a) Metabolic energy rate for walking and running as a function of speed, intersecting at speed $v = v_Q$. (b) The combined ‘effective cost curve’ is shown in orange, by picking the gait that has the lower cost at every relevant speed: resting at $v = 0$, walking below v_Q , and running above v_Q . Walking at speed v_B and running at v_C for different fractions of time results in an average metabolic rate as given by the line BC. When BC is the unique common tangent to the two curves, switching between B and C results in a lower average metabolic rate than is possible by exclusively walking or running (in fact the lowest possible for this model). This lowering of cost is possible because of the ‘non-convexity’ of the effective cost curve. (c) Hypothetical metabolic rate curves for walking and running that result in a ‘convex’ effective cost curve, implying no direct energetic benefit from walk–run mixtures.

ignoring, then considering the cost for transitions between walking and running.

3.2. Human locomotion energetics preliminaries

For the rest of this article, we will simply use the curves in figure 3a. The qualitative predictions are preserved as long as the curves have approximately the same shapes. We use the notation \dot{E} and ‘rate’ to refer to energy per unit time. The walking metabolic rate data \dot{E}_w is adequately fit by a quadratic function of speed [12,15]: $\dot{E}_w = a_0 + a_2 v^2$; we used $a_0 = 1.91 \text{ W kg}^{-1}$ and $a_2 = 1.49 \text{ W (ms}^{-1})^{-2}$. For running, while it is hard to statistically distinguish between linear [2,21] and quadratic models [14] using metabolic data, we used a quadratic model $\dot{E}_r = b_0 + b_1 v + b_2 v^2$, with $b_0 = 5.17 \text{ W kg}^{-1}$, $b_1 = 1.38 \text{ W (ms}^{-1})^{-1}$ and $b_2 = 0.34 \text{ W (ms}^{-1})^{-2}$ [13,14]. Finally, humans consume energy while resting (that is, not moving), modelled here as a constant rate $e_{\text{rest}} = 1.22 \text{ W kg}^{-1}$ [21].

We combine these three metabolic rates into an ‘effective cost curve’, shown in figure 3b, by picking the lower of the three rates at every speed; the resting rate is relevant only at $v = 0$.

3.3. Two choices: walk or run

In our experiment, the subjects had to cover a distance D_{required} in time T_{allowed} . For simplicity, say a subject runs for time duration $\lambda_r T_{\text{allowed}}$ at constant speed V_r and walks for a time duration $(1 - \lambda_r) T_{\text{allowed}}$ at constant speed V_w , such that she satisfies the distance, and, therefore, the average speed constraint of the experiment: $(1 - \lambda_r) T_{\text{allowed}} V_w + \lambda_r T_{\text{allowed}} V_r = D_{\text{required}}$. Here, the fraction of time spent running is λ_r , with $0 \leq \lambda_r \leq 1$. Rearranging, we have the average speed constraint

$$(1 - \lambda_r) V_w + \lambda_r V_r = \frac{D_{\text{required}}}{T_{\text{allowed}}} = V_{\text{avg}}.$$

Subject to this constraint, we wish to find V_w , V_r and λ_r so as to minimize the total energy expenditure E_{total} over the whole journey, first ignoring any costs for transients

$$E_{\text{total}} = [(1 - \lambda_r) \dot{E}_w(V_w) + \lambda_r \dot{E}_r(V_r)] T_{\text{allowed}}.$$

Minimizing E_{total} is equivalent to minimizing the average energy rate \dot{E}_{avg} over the total time duration: $\dot{E}_{\text{avg}} = E_{\text{total}}/T_{\text{allowed}} = (1 - \lambda_r) \dot{E}_w(V_w) + \lambda_r \dot{E}_r(V_r)$.

3.4. Optimal solution through the common tangent construction

Alexander [9] states the correct optimal strategies for the above problem, without a complete solution. Drummond [22] presents an elegant solution via the so-called ‘common tangent construction,’ as described below, while analysing a closely related exercise called ‘scout’s pace’ that mixes walking and running.

As in figure 3b, average speeds V_{avg} between speeds v_B and v_C can be obtained by walking at speed v_B and running at speed v_C . The average energy rate \dot{E}_{avg} for this walk–run mixture is given by the straight line between B and C, which is also the common tangent here. Because this straight line is below both cost curves, the mixture strategy has lower average energy rate compared with pure walking or running at such V_{avg} . Thus, a walk–run mixture is predicted by metabolic energy minimization for a range of intermediate speeds (between v_B and v_C). For $V_{\text{avg}} < v_B$, it is optimal to walk the entire distance. For $V_{\text{avg}} > v_C$, it is optimal to run the entire distance.

The necessary and sufficient condition for a walk–run mixture to be optimal for this model is that the effective cost curve (figure 3b) is *non-convex* near the intersection point Q. *Non-convexity*, by definition [23], means that we can draw a lower tangent to this effective cost curve that touches it at two points B and C as in figure 3b. To contrast with such non-convexity, we devised the hypothetical walking and running cost curves of figure 3c, which give rise to a *convex* effective cost curve, therefore implying no direct energy benefits from walk–run mixtures; the chord DE (corresponding to a walk–run mixture) is strictly above walking and running costs between D and E, and any lower tangent will touch the curve at only one point. See the electronic supplementary material, S1 for a discussion of convexity and related mathematics.

3.5. Three choices: walk, run or rest

In the above mathematical analysis and in our basic protocol experiments, the choice was between only walking and running. Arriving early and resting was not an option. If we allow resting, for low average speeds V_{avg} , a mixture of walking and resting becomes optimal.

The necessary and sufficient condition for the optimality of a walk–rest mixture is that the resting rate e_{rest} is strictly less than a_0 , the walking metabolic rate at infinitesimally small speeds (as is true for human walking [12]). This condition allows us to construct a lower tangent touching the walking cost curve at A, starting from the resting state

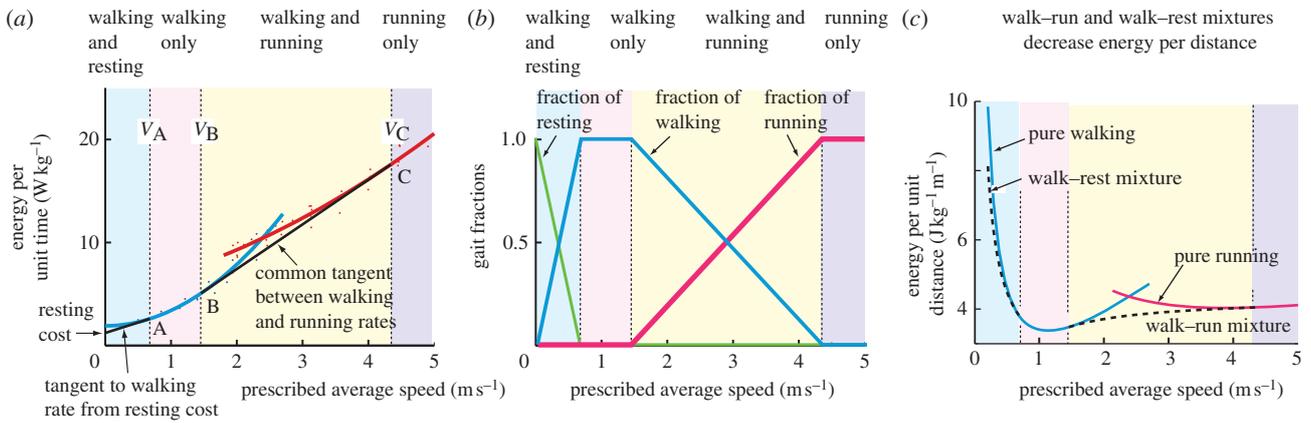


Figure 4. (a) Total metabolic rate as a function of walking and running speed, normalized by body mass, showing common tangent constructions for optimal walk–rest and walk–run mixtures. (b) Walk–run–rest fractions shown. As the average speed increases, the energy optimal strategy changes from a mixture of resting and walking to pure walking to a walk–run mixture to pure running. (c) Energy per unit distance for walking, running, walk–run mixtures and walk–rest mixtures. The mixture strategies (dotted lines) reduce the average energy per unit distance in the respective speed regimes, as shown. Note, the cost per distance of the mixtures is not a linear function of average speed, which is why the ‘common tangent construction’ is performed on the cost per time curves.

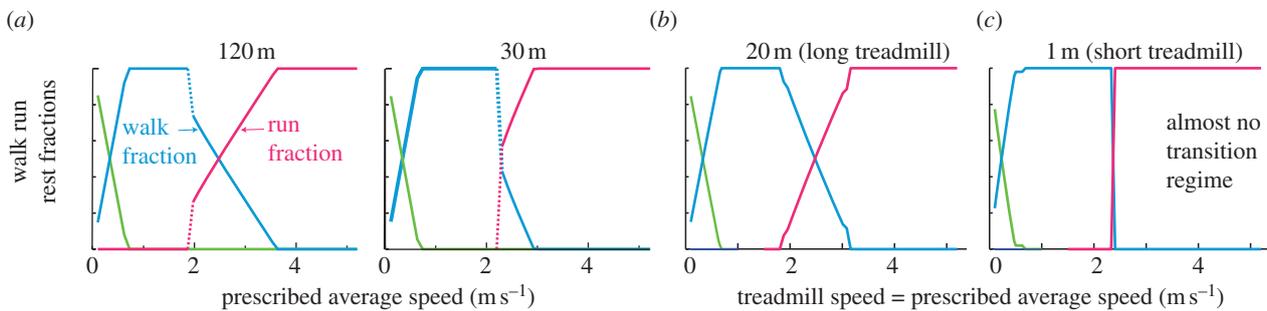


Figure 5. Effect of adding energy cost for transients: model predictions from numerical optimizations. (a) When travelling a finite distance overground, the extent of the walk–run transition regime depends on the distance travelled ($D_{\text{required}} = 120$ and 30 m shown). Smaller distances have smaller transition regimes. (b) When having to remain on a constant-speed treadmill of finite length, the extent of the walk–run transition regime depends on the treadmill length. For long treadmills (e.g. 20 m), there is a substantial walk–run mixture regime. On very short treadmills (e.g. 1 m), essentially no walk–run mixture regime exists, and the transition from all walking to all running is sharp.

(0, e_{rest}), as shown in figure 4a. Then, for $V_{\text{avg}} < V_A$, a mixture of resting and walking at V_A is optimal; note, $V_A = \sqrt{(a_0 - e_{\text{rest}})/a_2}$. This V_A is also the constant walking speed that minimizes the ‘net’ energy cost per unit distance $E'_{\text{net}} = (a_0 - e_{\text{rest}} + a_2 v^2)/v$ without time constraints [8].

Figure 4a consolidates the predictions of metabolic energy minimization, showing the four average speed regimes with their respective optimal behaviours: walk–rest mixtures (with walking at V_A), constant speed pure walking (walk at V_{avg}), walk–run mixtures (walking at V_B , running at V_C), and constant speed pure running (run at V_{avg}). Figure 4b shows the predicted optimal fractions of resting, walking and running. Figure 4c shows how the walk–rest and walk–run mixtures reduce the energy per unit distance $E' = \dot{E}_{\text{avg}}/V_{\text{avg}}$ over pure walking and running. Note that the walking speeds V_A and V_B are not equal to, but are, respectively, less than and greater than the maximum range speed, which minimizes the cost per unit distance for walking [8].

3.6. Costs for transients, the number of switches and finite distances

In the analysis thus far, we have assumed that the energy rate is purely a function of speed and gait, assuming that neither changing speeds nor switching gaits entail an energy cost. Such transients do have a cost, associated with a change in

kinetic energy or limb movement patterns [24]. Without these costs for transients, the above model implies that one can switch between gaits arbitrarily often without affecting the optimality of the walk–run mixture, as long as the walking and running fractions are unchanged.

As soon as a cost for transients is added to the mathematical model, say, proportional to change in kinetic energy, having exactly one switch between walking and running, or exactly one switch between walking and resting, becomes optimal. In the electronic supplementary material, §S2, we describe numerical optimization to obtain the energy optimal gait strategies in the presence of a cost for transients, shown in figure 5a. Thus, we find that despite transient costs, the qualitative picture of figure 4a,b is preserved, but the specific transition speeds separating the various regimes are slightly changed and depend on D_{required} (see the electronic supplementary material, figure S3 expands on figure 5a). The effect of transient costs become negligible over much larger distances, again giving figures 4a,b.

3.7. Locomotion on long treadmills with transient costs

Unlike short treadmills, long treadmills allow larger voluntary speed fluctuations while imposing an average speed constraint over the long term. For treadmill locomotion, there is no explicit time constraint or distance constraint, but only a constraint that the person remains on the treadmill. In the absence of transient

costs, the energy optimal strategies for remaining on the treadmill are exactly as in figure 4. However, with transient costs, substantial walk–run mixtures become optimal only when the treadmill is long enough. This treadmill-length-dependence of transition speeds is shown in figure 5*b* (also in electronic supplementary material, figure S4 for greater detail). These figures were obtained using numerically computed optimal walk–run–rest mixtures, subject to the constraint that the person remains within the treadmill; the numerical computation is documented in more detail in the electronic supplementary material, §S3. Thus, if the goal is to simply *stay* on a long treadmill (e.g. an airport moving walkway), instead of traversing it, energy minimization predicts that humans will walk or run in place for some speeds, but use walk–stand or walk–run mixtures at other speeds, moving against the belt some of the time.

4. Discussion

4.1. Numerical predictions from our model

We are able to explain the qualitative features of walk–run mixtures using energy minimization. Using cost curves from different authors [2,12–15,21,21] will result in slightly different numerical predictions, by as much as 0.2 m s^{-1} for each of the predicted transition speeds. Also, averaging cost curves across subjects can move transition points. Ideally, one should use subject-specific energy rate curves and test if a subject's gait choice is consistent with her specific energetics. For our assumed cost curves and no transient costs (equivalent to traveling a very large distance), we obtained $V_A = 0.7 \text{ m s}^{-1}$, $V_B = 1.45 \text{ m s}^{-1}$, and $V_C = 4.35 \text{ m s}^{-1}$ (figure 4). With transient costs and $D_{\text{required}} = 120 \text{ m}$, we obtained $V_A = 0.7 \text{ m s}^{-1}$, $V_B = 1.9 \text{ m s}^{-1}$, and $V_C = 3.6 \text{ m s}^{-1}$ (figure 5*a*); this predicted walk–run transition region overlaps with those in figure 1.

The speed V_C in figures 4 and 5 is sensitive to the curvature of the quadratic running cost model, approaching the maximum running speed for a linear model (which still predicts walk–run mixtures). Because humans never use maximum running speeds, perhaps the running rate is indeed slightly curved (assuming energy minimization, not fatigue, determines speeds). The slight curvature used here is consistent with metabolic data [13,14]. We ignored other complexities in the energy models, e.g. post-exercise increases in energy and oxygen consumption [25].

4.2. Higher variability near transition

Behavioural variability in the running fractions of figure 1*a–c* is higher near the gait transition region than away from it (figure 6). A few plausible mechanisms could contribute to such variability: (i) within-subject variability, perhaps due to sensory or computational noise in the human motor system in deciding which gait to use; because the walking–running costs are most similar near the transition, the errors could be higher; (ii) subjects using the correct optimal fraction for an incorrect average speed (with a given speed error) will produce variability proportional to the absolute slope of the running fraction curve $\lambda_r(v)$, maximum at the transition; (iii) pooling different subjects with slightly different running fraction curves shifted sideways will also produce variability proportional to the absolute slope of the running fraction curve. See the electronic supplementary material, §S5 for a related mathematical note.

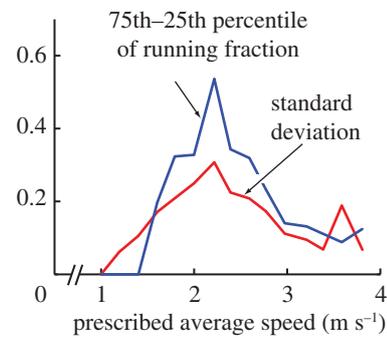


Figure 6. Two measures of variability in running fractions from figure 1*a*. Variability is maximal in the transition region, where the running fraction also has the greatest slope.

4.3. Other overground experiments

Recently, some non-treadmill overground gait transition experiments were performed, in which subjects were asked to walk with increasing speed and then start running when they found it natural (e.g. [26] found a transition speed of 2.85 m s^{-1} , with 0.5 m s^{-2} natural acceleration). In contrast, in our more ecological experiment, we did not explicitly suggest increasing speeds or gait change, allowing more choice as in daily legged travel.

Also, Hoyt & Taylor [27] and Pennycuik [28] observed double-peaked speed distributions in free-ranging animals, but there were no explicit average speed constraints in such contexts.

4.4. Alternative non-energy-based explanations

Partly to address the slight discrepancy between energy optimality and the treadmill gait transition speed, a number of non-energy-based kinematic and kinetic factors have been posited as triggering the transition [6,29–35]—usually suggesting that humans switch to running because some force, strain, velocity or stability threshold is violated while walking. None of these intra-stride threshold-based hypotheses, as stated, can explain why humans use a walk–run mixture when there is no strict speed constraint. Further, unlike energy minimization, which predicts many phenomena related to human locomotion at least qualitatively [9,11], these other hypotheses have been not systematically tested for phenomena other than gait transitions.

We mention two further alternate hypotheses. First, perhaps subjects have poor time-to-destination estimation, so that the subjects initially start to walk and then run when they realize they have very little time left (or the reverse), but it is unclear how this could explain various systematic trends in our experiments without additional assumptions. Second, we can rule out fatigue as a reason for switching to walking after running for a while, as subjects were able to run the whole way at higher speeds in other trials. Also, our trials were short enough that fatigue is unlikely to be an issue. On the other hand, in the presence of fatigue, multiple switches between walking and running may well become favourable [22]. For instance, some animals use intermittent locomotion to extend their endurance [36] at high average speeds, while briefly exceeding their maximum aerobic speed.

Finally, while we have focused on energy minimization to explain trends, we recognize that animals must trade-off energy minimization with other constraints and goals [9]. Our implicit assumption is that the cost curves used here are for movements that have already taken such trade-offs into account.

4.5. What energy should we minimize?

We have assumed that subjects minimize the total energy cost over the experimentally allowed task duration (equivalently, the whole day [8]). Instead, if humans minimize the energy to arrive at the destination, not counting resting after arriving, the predictions for large distances are identical to figure 4*a,b* except the walking speed V_A in a walk–rest mixture is replaced by the so-called *maximum range speed*, the minimum in figure 4*c*, given by $\sqrt{a_0/a_2}$, typically 1.2–1.4 m s⁻¹ [8].

Also, in their daily life, instead of minimizing energy subject to a time constraint, it may be that humans trade-off a cost for time and energy, resulting in slightly higher speeds than predicted by pure energy optimality [37].

4.6. When should we minimize energy?

In future work, we suggest repeating our experiments over a range of distances, including much shorter (25 m, say) and much longer distances (3 km, say), to test if the results in figures 1 and 2, and other behaviour, change systematically. Over much longer distances, without practise and visual landmarks, perhaps humans will have greater difficulty judging time and distance to destination, and as a consequence, perhaps there will be greater behavioural variability.

It is sometimes argued that over short distances, humans and other animals may not move in a manner that minimizes energy because this energy would be a small fraction of the daily energy budget [38]. While plausible, this hypothesis has not been tested systematically. Below, we provide a few inter-related reasons for why humans may minimize energy even at short travel distances considered here.

First, we have shown empirically that over relatively short distances of 100 m, human behaviour seems qualitatively consistent with energy minimization. At least for steady walking, there are no major observed differences in how people walk a short distance versus a much longer distance (in the absence of fatigue); so the same principles may underlie walking both short and longer distances. Further, the walk–run strategy for minimizing energy over many thousand metres is the same as the walk–run strategy for minimizing the energy for a few hundred metres (with minor quantitative differences). Thus, one does not have to evolve or learn qualitatively different strategies for different distances.

Finally, we note that energy is a ‘fungible’ quantity. That is, metabolic energy saved in one task is available for use in any other task. (Fungibility is an economics concept, used most commonly as a descriptive property of money.) In the absence of other trade-offs and constraints, evolutionary processes could not differentiate between energy saved in one big task versus a hundred small tasks. Thus, energy reductions in the hundred small tasks might be as likely as in the one big task, if we controlled for the complexity of the two sets of tasks. To be sure, it is possible for human motor behaviour to be inconsistent with the fungibility of energy, just as there is evidence from behavioural economics that spending behaviour is sometimes inconsistent with the fungibility of money [39]. This is an open question for future empirical study.

4.7. Cognitive and motor mechanisms governing gait choice.

While we do not know how humans adjusted their gait strategy in our experiments, we see evidence of both feedback and feed-forward mechanisms [40]. In the short T_{allowed} trials, the subjects

realize immediately that they have to run relatively fast to arrive on time, suggesting feed-forward mechanisms that convert the cognitively provided distance–time constraints into gait. And later in each trial, the subjects typically speed up or slow down to correct for earlier misestimations of the speed required, suggesting feedback mechanisms.

5. Related phenomena, conjectures and other applications

In this section, we discuss related situations that might benefit from similar models, make conjectures partly informed by available energy data, suggesting future experiments.

5.1. Moving walkways

Say the goal is to go from one end of a very long treadmill (e.g. an airport moving walkway) to the other, instead of just staying on the treadmill. If the goal speed is 1.2 m s⁻¹ (say) relative to the ground, a walkway speed of 0.7 m s⁻¹ requires 0.5 m s⁻¹ relative to the walkway, at which average speed a walk–rest mixture may be optimal. Thus, we conjecture that faster walkways may promote more standing, possibly resulting in congestion and reduced people transport (see [8] for a similar conjecture).

5.2. Keeping up with someone else: human children, animals on a leash, etc.

Human children have a lower walk–run transition speed than adults. Extrapolating children’s gait transition data in Tseh *et al.* [17] suggests that children with leg length of 50–55 cm will have a transition speed of about 1.4 m s⁻¹, close to adult preferred walking speeds. Thus, while travelling with a parent at 1.4 m s⁻¹, a small child might benefit energetically from a walk–run mixture; the walking–running cost curves for slightly older children [41] continue to show the necessary non-convexity, but such data are not available for very small children. We speculate that this energy benefit may get reflected in the child walking slowly and then running to catch up or overtake the parent, sometimes leading or lagging. While children’s activity is often burst-like [42], we do not know of parent–child co-locomotion studies.

Similarly, dogs transition from walking to trotting between 0.9 and 1.3 m s⁻¹ depending on size [43]. While we could not find walking–trotting energy data for dogs, we see evidence of the energy non-convexity necessary for walk–trot mixtures in horses and goats [27,44]. Extrapolating from these quadrupeds, we conjecture that dogs on a long leash, accompanying a walking human, might benefit from walk–trot mixtures (as might goats and horses at other speeds).

Finally, when animals (whose juveniles benefit from adult protection) migrate, juveniles and adults often travel long distances at the same average speed. For such animals, the adult’s maximal range speed may (if the speeds so conspire and given the necessary non-convexity) correspond to a mixture of gaits for a juvenile, or vice versa. Such behaviour is not necessary, of course. For instance, both adult and juvenile gnus apparently use a mixture of walking and cantering [28].

5.3. Animals on very slow treadmills

Various untrained animals, especially small animals, when placed on a slow treadmill, sometimes perform a mixture of

standing still, coasting to the back of the treadmill, and then scooting forward, giving the impression of being hard to train; researchers often have to use some stimulation to get the animal to move steadily [45]. We conjecture that some of this behaviour could be due to the energy optimality of walk–rest mixtures. Recall that the necessary condition for such optimality is that the resting cost be less than the extrapolated locomotion cost at zero speed, documented for white rats by Schmidt-Nielsen [46].

5.4. Walk faster if you can lie down at the end

So far, we have used a single resting energy rate e_{rest} . Given that standing, sitting and lying down have progressively lower energy costs [47], energy minimization over the whole time duration implies, surprisingly, a higher walking speed in walk–rest mixtures if the subject is allowed to lie down on arrival than if the subject is allowed to only stand on arrival. See the electronic supplementary material, figure S5. We have not extensively explored experimental protocols involving rest, except the arriving-early variant in figure 1c, in which subjects did arrive early when T_{allowed} was large. Also, the experiment needed to test the above prediction may not be very ecological.

5.5. Altered body or environment

The walking and running cost curves, in humans and in other animals, are affected by changes either to the body or to the environment (e.g. wearing a loaded backpack, going uphill or downhill, altered gravity). The predicted speed regime corresponding to optimality of a walk–run mixture will be affected by such changes, which can be tested by repeating the experiments herein in those altered circumstances.

5.6. Marathoners, hunters and soccer players

During marathons and ultra-marathons, runners sometimes use a walk–run mixture [48], partly explained by fatigue. But note that the average US marathon finish times including non-elite runners are 4.5–5 h, with average speeds of 2.3–2.6 m s⁻¹, when a walk–run mixture is energetically beneficial, as pointed out earlier by Alexander [9] and Drummond [22]. Analogously, humans that run 10-min miles (2.7 m s⁻¹) might need less energy using walk–run mixtures (extrapolating figure 4a).

Human ‘persistence hunters’ pursue prey for many hours, mixing running and tracking the animal. Hunts witnessed by Liebenberg [49] in the Kalahari averaged 1.75 m s⁻¹. While energy-minimizing humans might mostly walk with a small running fraction at these average speeds (using figure 1a or 4b), it may be worthwhile to study the gait fractions used by the hunters, likely different from energy optimal owing to hunting constraints (like keeping up with the animal), resulting in extra energetic cost.

Analogously, over a 90-min game, soccer players average about 2.1 m s⁻¹ [50]. Given various game-play constraints (defending, intercepting, etc.), which clearly supersede energy conservation, one might quantify the extra energy such constraints impose, over and above the minimum energy required at the observed average speed; also of interest may be the speed and gait distributions.

5.7. Other transport modes: flying, swimming and driving

Finally, we remark that the optimality of mixture strategies may not be exclusive to legged locomotion. For instance, bounding

flight in small birds, the intermittent swimming of mammals, and extreme accelerate–coast mixtures in some cars (also called burn and coast, or pulse and glide), especially those that participate in ‘eco-marathon’ races, have been argued to reduce energy consumption [51–53]. It may also be of interest to see whether legged robot locomotion cost curves have the necessary non-convexity, implying energetic benefits for using gait mixtures.

6. Conclusion

We observed that humans use a walk–run mixture at intermediate average locomotion speeds and argued that this behaviour is consistent with energy optimality. We have commented on possible application of the ideas to superficially diverse phenomena in humans and other animals. Exploring these related phenomena (and the underlying assumptions) quantitatively with controlled experiments and using subject-specific energy measurements for the mathematical models would enable us to better understand the limitations of energy minimization as a predictor of animal movement behaviour.

7. Material and methods

The protocols were approved by the Ohio State University’s Institutional Review Board. Subjects participated with informed consent. The subjects’ ($n = 36$, aged 20–32, eight female) had mean body mass 74.2 kg (12 kg s.d.) and mean height 1.79 m (0.078 m s.d.).

7.1. Basic experimental protocol

The outdoor subjects ($n = 19$) used a relatively straight and horizontal sidewalk. The indoor subjects ($n = 9$) performed them in a 2.5 m wide building corridor. Total distance was $D_{\text{required}} = 122$ m. We used 15 different total times T_{allowed} , giving average speeds of 1 to 3.8 m s⁻¹: 32, 34, 36, 38, 41, 44, 47, 51, 55, 61, 68, 76, 87, 102 and 122 s, presented in a random sequence. The subjects had no practice trials specific to these time durations except for a single initial practice trial to ensure protocol understanding. All subjects wore a watch (Garmin Forerunner 305) that recorded stride frequency from a pedometer (Garmin footpod). Some outdoor subjects ($n = 10$) carried a high-end GPS unit (VBOX Mini, Racelogic UK) to measure speed accurately. See the electronic supplementary material for more details about the subject population, protocol and instrumentation. The outdoor experiment required the subject to travel in only one direction from S to E. In the indoor experiment, S and E coincided and the subject turned back midway.

7.2. Variants of the basic protocol

We performed minor variants of the basic protocol for a total of $n = 8$ subjects. For $n = 3$ subjects, we repeated each speed three times, for a total of five speeds in random sequence. For $n = 2$ subjects, each of 10 average speed trials had a different distance, ranging from 70 to 250 m. For $n = 2$ subjects, subjects could arrive earlier than T_{allowed} . For one subject, we used a fixed longer distance 244 m for all trials.

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