

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

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Abstract

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 stop-watch 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 traveling finite distances and for traveling 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.

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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 treadmill switches to running when the treadmill speed is slowly increased [25, 45, 19]. 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 [49]. 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 [30]). 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 end point E, separated by a distance D_{required} , in a given time duration T_{allowed} . The subjects carried a stop-watch 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 end point exactly when the stop-watch 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. All subjects were video-taped and instrumented for stride frequency. Some subjects were instrumented for speed. 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 *Materials and Methods* at the end of this article and *Supporting Information* (section 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% 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 [14]. In walking, the hip vaults over on the leg more like an inverted pendulum and at least one foot always contacts the ground [42].

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 (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 in Figure 1a, which is close to, but slightly higher than the treadmill gait transition speeds in the

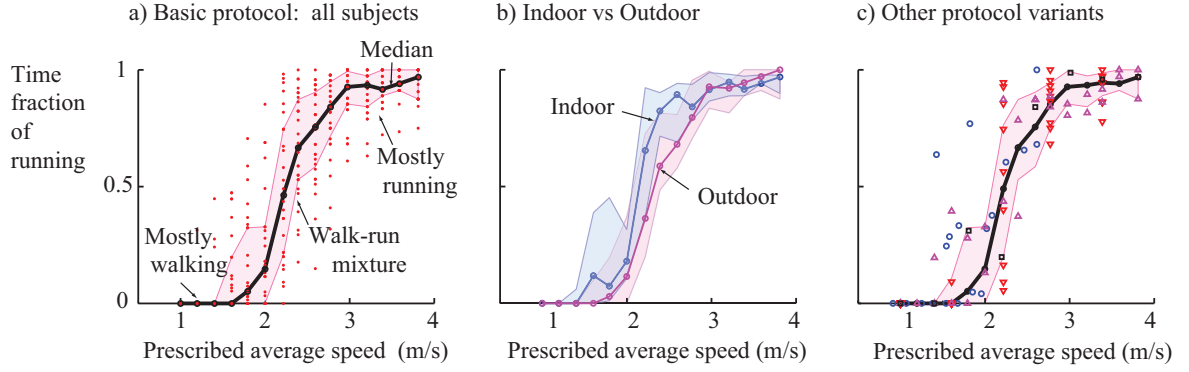


Figure 1: a) All subjects with the basic protocol ($N = 28$ subjects, indoor and outdoor, $D_{\text{required}} = 122$ m). The time fraction of running is shown: the red dots are the raw data (each dot is a trial, all data points shown), the solid black line is the population median, and the pink band denotes 50% of the data centered around the median (25th to 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 3 trials per prescribed average speed for five different prescribed average speeds (red triangles, ∇), in which the trials had different random distances ranging between 70 m and 250 m and different time allowed's (blue circles, \circ), in which the subject traveled twice the distance, 244 m (black squares, \square), and in which the subjects were allowed to arrive earlier than T_{allowed} (magenta triangles, \triangle).

literature [45, 19]. At the highest average speeds, the running fraction is not quite 100%, 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 perceived speed, shifting the actual gait transition region to lower speeds [40, 30]. The data from the protocol variants, taken as a whole, are not qualitatively different from the basic protocol (Figure 1c); 75% of the protocol variants' data points fell within the centered 50% 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. Such double-peaked distributions indicate (many) subjects walking slow and running fast in a walk-run mixture. At $V_{\text{avg}} = 2$ m/s, the lower speed walking peak has 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 $V_{\text{avg}} = 2.97$ m/s, when subjects ran most of the time. For V_{avg} below 2 m/s and above 3 m/s, 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 5 subjects, for the $V_{\text{avg}} = 2.39$ m/s trial, which is in the walk-run transition region. For three subjects shown (subjects 4-6),

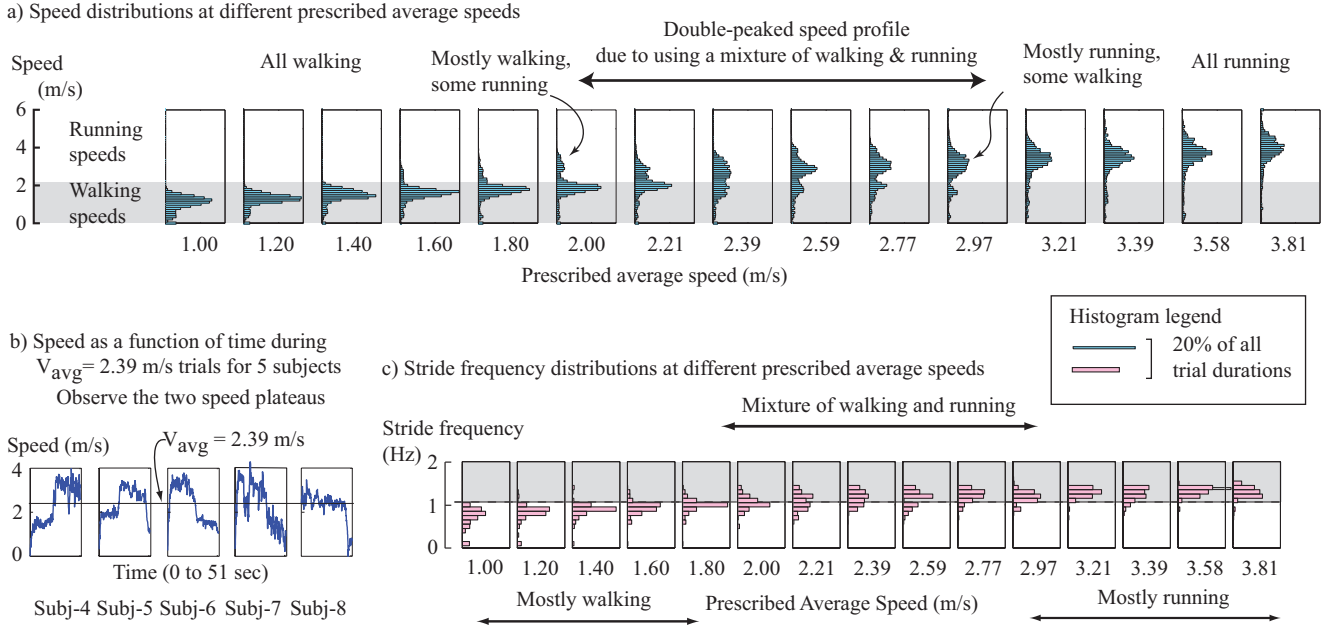


Figure 2: a) Histograms of the speeds at which the subjects travelled during each of the 15 trials with different prescribed average speeds V_{avg} ; pooled over the 10 subjects with GPS speed measurements, with histogram bin width = 0.1 m/s. The histograms have a single peak for low and high prescribed 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 $V_{avg} = 2.39$ m/s and $T_{allowed} = 51$ 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 gray band across the histograms (panels a and c) indicating normal walking and running speeds or frequencies is simply to guide the eye, not meant to be a strict separator.

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 2-3 m/s) 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 *Supplementary Information*).

3 Energy minimization as a candidate theory of gait choice

3.1 On a treadmill, switch to save energy

Margaria and others [25] 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 [2, 28, 42, 41]. Example walking and running metabolic rates as functions of speed, based on published data [5, 50, 29, 43], 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 [19, 46, 44] found a small difference (~ 0.1 m/s) 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 [19]), others

[27, 32] did not; see [2, 8] for possible explanations.

We now describe what metabolic energy minimization predicts in the context of our non-treadmill experiment, first ignoring, then considering the cost for transitions between walking and running.

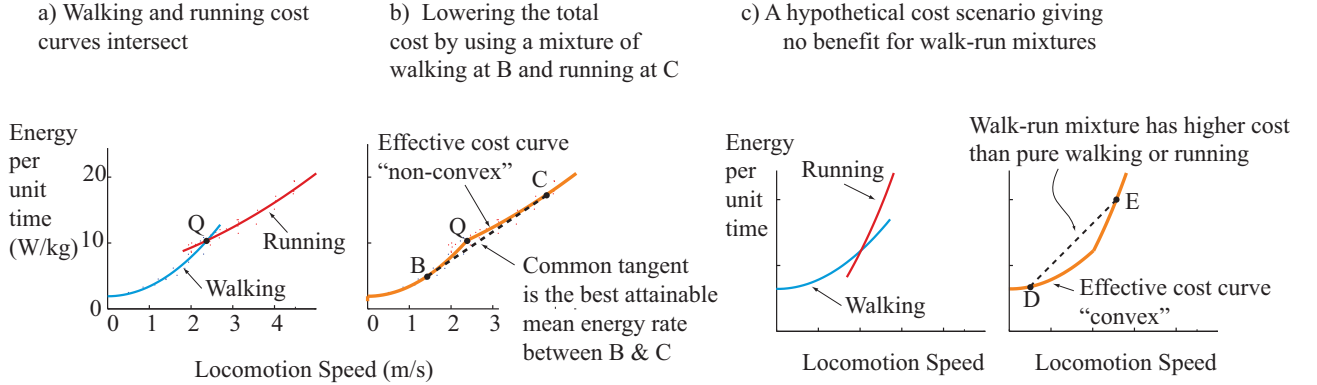


Figure 3: a) Metabolic energy rate for walking and running as a function of speed, intersecting at speed $v = V_Q$. b) The combined “effective cost curve” is shown in orange, by picking the gait that has the lower cost at every relevant speed: resting at $v = 0$, walking below V_Q , and running above 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.

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 [5, 50]: $\dot{E}_w = a_0 + a_2 v^2$; we used $a_0 = 1.91$ W/kg and $a_2 = 1.49$ W/(ms⁻¹)². For running, while it is hard to statistically distinguish between linear [25, 15] and quadratic models [43] using metabolic data, we used a quadratic model $\dot{E}_r = b_0 + b_1 v + b_2 v^2$, with $b_0 = 5.17$ W/kg, $b_1 = 1.38$ W/(ms⁻¹), and $b_2 = 0.34$ W/(ms⁻¹)² [29, 43]. Finally, humans consume energy while resting (that is, not moving), modeled here as a constant rate $e_{\text{rest}} = 1.22$ W/kg [15].

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: $(1 - \lambda_r) T_{\text{allowed}} \cdot V_w + \lambda_r T_{\text{allowed}} \cdot V_r = D_{\text{required}}$. Here, the fraction of time spent running is λ_r , with $0 \leq \lambda_r \leq 1$. Rearranging, we have the average speed constraint:

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

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:

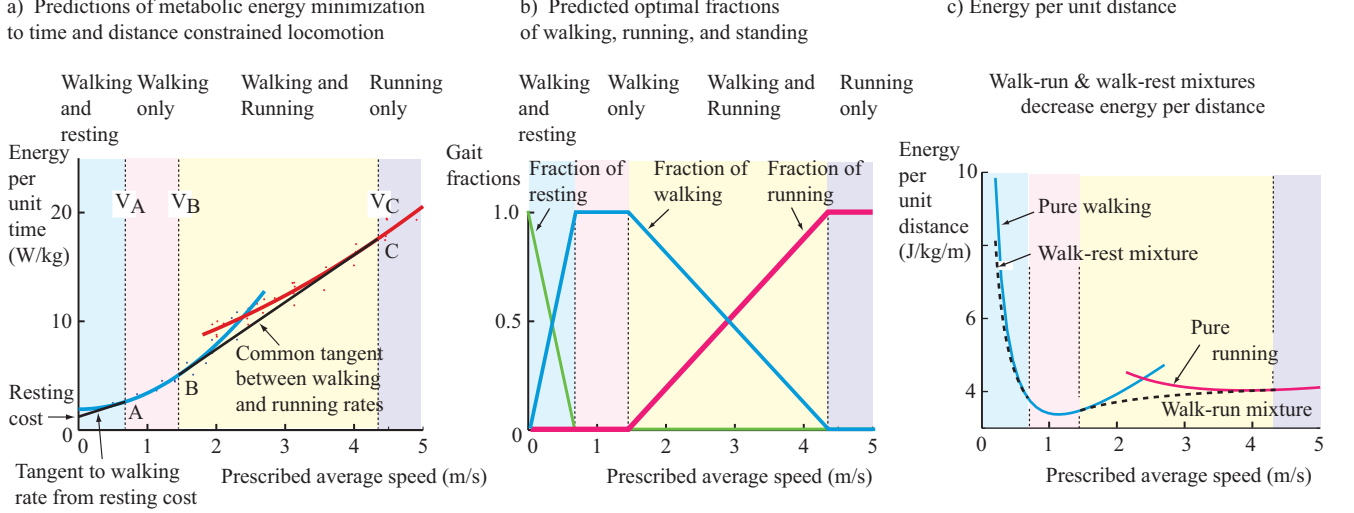


Figure 4: a) Total metabolic rate as a function of walking and running speed, normalized by body mass, showing common tangent constructions for optimal walk-rest and walk-run mixtures. b) Walk-run-rest fractions shown. As the average speed increases, the energy optimal strategy changes from a mixture 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.

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

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

3.4 Optimal Solution through the Common Tangent Construction

Alexander [2] states the correct optimal strategies for the above problem, without a complete solution. Drummond [10] presents an elegant solution via the so-called ‘common tangent construction,’ as described below, while analyzing a closely related exercise called “scout’s pace” which 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 to 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 [37], 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. In contrast, the hypothetical walking and running cost curves of Figure 3c give rise to a *convex* effective cost curve, which implies 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 *Supplementary Information* (section 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 [5]). This condition allows us to construct a lower tangent touching the walking cost curve at A, starting from the resting state $(0, e_{\text{rest}})$, 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 [40].

Figure 4a consolidates the predictions of metabolic energy minimization, showing the four average speed regimes with their respective optimal behaviors: 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 $E' = \dot{E}/V_{\text{avg}}$ over pure walking and running.

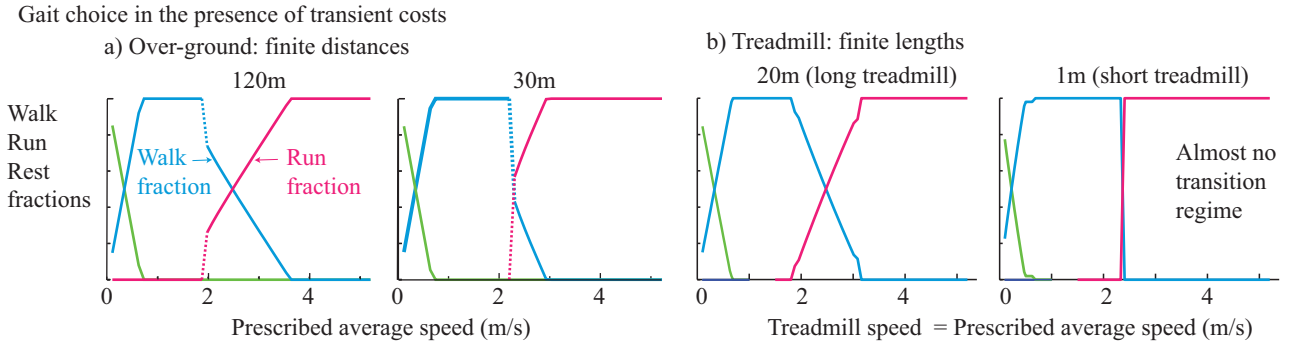


Figure 5: Effect of adding energy cost for transients: model predictions from numerical optimizations. a) When traveling a finite distance overground, the extent of the walk-run transition regime depends on the distance travelled ($D_{\text{required}} = 120$ m and 30 m shown). Smaller distances have 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.

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 [48]. 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 *Supporting Information* (section 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} (*Supplementary Information* 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. In the absence of transient costs, the energy optimal strategies for remaining on the treadmill are exactly as in Figures 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 5b (also 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 *Supporting Information* (section 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

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 [15, 5, 50, 29, 25, 15, 43] will result in slightly different numerical predictions, by as much as 0.2 m/s 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 $V_A = 0.7$ m/s, $V_B = 1.45$ m/s, and $V_C = 4.35$ m/s (Figure 4). With transient costs and $D_{\text{required}} = 120$ m, we obtained $V_A = 0.65$ m/s, $V_B = 2$ m/s, and $V_C = 3.55$ m/s (Figure 5a); this predicted walk-run transition region overlaps with those in Figures 1.

The speed V_C in Figures 4-5 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 [29, 43]. We ignored other complexities in the energy models. e.g., post-exercise increases in energy and oxygen consumption [26].

Higher variability near transition. Behavioral variability in the running fractions of Figure 1a-c is higher near the gait transition region than away from it; see Figure 6. A few plausible mechanisms could contribute to such variability: (1) 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; (2) 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; (3) pooling different subjects with slightly different transition curves shifted sideways will also produce variability proportional to the slope of the transition curve. See *Supplementary Information* (section S5) for a related mathematical note.

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., [7] found a transition speed of 2.85 m/s, with 0.5 m/s² 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.

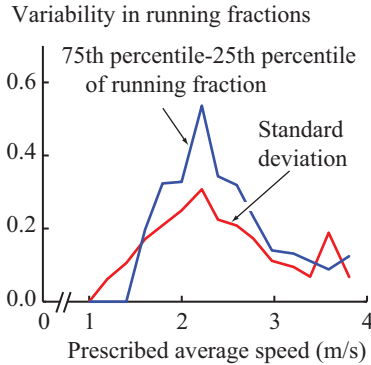


Figure 6: Two measures of variability in running fractions from Figure 1a. Variability is maximal in the transition region, where the running fraction also has the greatest slope.

Also, Hoyt, Taylor and Pennycuik [18, 33] observed double-peaked speed distributions in free-ranging animals, but there were no explicit average speed constraints in such contexts.

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 [16, 35, 36, 31, 47, 14, 20, 11] — 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 [2, 41], 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 favorable [10]. For instance, some animals use intermittent locomotion to extend their endurance [52] 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 [2]. Our implicit assumption is that the cost curves used here are for movements that have already taken such trade-offs into account.

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 [40]). 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 4a-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 4c, given by $\sqrt{a_0/a_2}$, typically 1.2-1.4 m/s [40].

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 [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 1-2, and other behavior, change systematically. Over much longer distances, without practice and visual landmarks, perhaps humans will have greater difficulty judging time and distance to destination, and as a consequence, perhaps there will be greater behavioral 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 (e.g., [13]). 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 a hundred meters, human behavior 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 meters is the same as the walk-run strategy for minimizing the energy for a few hundred meters (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 behavior to be inconsistent with the fungibility of energy, just as there is evidence from behavioral economics that spending behavior is sometimes inconsistent with the fungibility of money [17]. This is an open question for future empirical study.

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 [21]. 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 mis-estimations 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.

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 (say) relative to the ground, a walkway speed of 0.7 m/s requires 0.5 m/s 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 [40] for a similar conjecture).

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 [46] suggests that children with leg length of 50-55 cm will have a transition speed of about 1.4 m/s, close to adult preferred walking speeds. Thus, while traveling with a parent at 1.4 m/s, a small child might benefit energetically from a walk-run mixture; the walking-running cost curves for slightly older children [24] continue to show the necessary non-convexity, but such data is 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 [3], 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 depending on size [4]. 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 [18, 34]. Extrapolating from these quadrupeds, we conjecture that dogs on a long leash 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 behavior is not necessary, of course. For instance, both adult and juvenile gnus apparently use a mixture of walking and cantering [33].

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 (e.g., [9]). We conjecture that some of this behavior 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 in [39].

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 (see [1]), 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 *Supplementary Information* (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.

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.

Marathoners, hunters, soccer players. During marathons and ultra-marathons, runners sometimes use a walk-run mixture [12], partly explained by fatigue. But note that the average US marathon finish times including non-elite runners are 4.5-5 hours, with average speeds of 2.3-2.6 m/s, when a walk-run mixture is energetically beneficial, as pointed out earlier by [10, 2]. Analogously, humans that run 10 minute miles (2.7 m/s) 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 [23] in the Kalahari averaged 1.75 m/s. 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 due to hunting constraints (like keeping up with the animal), resulting in extra energetic cost.

Analogously, over a 90-minute game, soccer players average about 2.1 m/s [38]. 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.

Other transport modes: Flying, Swimming, 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, 22].

6 Conclusion

We observed that humans use a walk-run mixture at intermediate average locomotion speeds and argued that this behavior 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 behavior.

Materials 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, 8 female) had mean body mass 74.2 kg (12 kg standard deviation) and mean height 1.79 m (0.078 m standard deviation).

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 fifteen different total times T_{allowed} , giving average speeds of 1 to 3.8 ms^{-1} : 32, 34, 36, 38, 41, 44, 47, 51, 55, 61, 68, 76, 87, 102, and 122 seconds, 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 *Supplementary Information* 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.

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 3 times, for a total of 5 speeds in random sequence. For $N = 2$ subjects, each of 10 average speed trials had a different distance, ranging from 70 m 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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References

- [1] AINSWORTH, B. E., HASKELL, W. L., WHITT, M. C., IRWIN, M. L., SWARTZ, A. M., STARTH, S. J., O’BRIEN, W. L., D. R. BASSETT, J., SCHMITT, K. H., EMPALNCOURT, P. O., JR., D. R. J., AND LEON, A. S. Compendium of physical activities: an update of activity codes and met intensities. *Med. Sci. Sports Exerc.* 32, Suppl. (2000), S498–S516.
- [2] ALEXANDER, R. M. Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* 69 (1989), 1199–1227.

- [3] BAILEY, R. C., OLSON, J., PEPPER, S. L., PORSZASZ, J., BARSTOW, T. J., AND COOPER, D. M. The level and tempo of children’s physical activities: an observational study. *Med. Sci. Sports Exer.* 27 (1995), 1033–1041.
- [4] BLASZCZYK, J. Gait transitions during unrestrained locomotion in dogs. *Equine Vet J* 33, S33 (2001), 112–115.
- [5] BOBBERT, A. C. Energy expenditure in level and grade walking. *J. Appl. Physiol* 15 (1960), 1015–1021.
- [6] BORNSTEIN, M. H., AND BORNSTEIN, H. G. The pace of life. *Nature* 259 (1976), 557–558.
- [7] CAEKENBERGHE, I. V., SMET, K. D., SEGERS, V., AND CLERCQ, D. D. Overground vs. treadmill walk-to-run transition. *Gait Posture* 31 (2010), 420–428.
- [8] DIEDRICH, F. J., AND W. H. WARREN, J. Why change gaits? dynamics of the walk-run transition. *J. Exp. Psychol: Hum Percep Perf* 21 (1995), 183–202.
- [9] DISHMAN, R. K., ARMSTRONG, R. B., DELP, M. D., GRAHAM, R. E., AND DUNN, A. L. Open-field behavior is not related to treadmill performance in exercising rats. *Physiol Behav* 43 (1988), 541–546.
- [10] DRUMMOND, J. E. The mathematics of scout’s pace. *Math. Gazette* 70 (1986), 185–190.
- [11] FARRIS, D. J., AND SAWICKI, G. S. Human medial gastrocnemius force-velocity behavior shifts with locomotion speed and gait. *PNAS* 109 (2012), 977–982.
- [12] GALLOWAY, J. *Marathon: You Can Do It!* Shelter Publications, 2010.
- [13] GARLAND, T. Scaling the ecological cost of transport to body mass in terrestrial mammals. *American Naturalist* (1983), 571–587.
- [14] GEYER, H., SEYFARTH, A., AND BLICKHAN, R. Compliant leg behaviour explains basic dynamics of walking and running. *Proc. R. Soc. B* 273 (2006), 2861–2867.
- [15] GLASS, S., AND DWYER, G. B. *ACSM’S metabolic calculations handbook*. American College of Sports Medicine, 2006.
- [16] HANNA, A., ABERNETHY, B., NEAL, R. J., AND BURGESS-LIMERICK, R. Triggers for the transition between human walking and running. In *Energetics of human activity*, W. A. Sparrow, Ed. Human Kinetics, 2000, pp. 124–164.
- [17] HASTINGS, J., AND SHAPIRO, J. M. Mental accounting and consumer choice: Evidence from commodity price shocks. *NBER Working Paper No. 18248* (2012).
- [18] HOYT, D. F., AND TAYLOR, C. R. Gait and the energetics of locomotion in horses. *Nature* 292 (1981), 239–240.
- [19] HRELJAC, A. Preferred and energetically optimal gait transition speeds in human locomotion. *Med. Sci. Sports Exerc.* 25 (1993), 1158–1162.
- [20] HRELJAC, A. The relationship between joint kinetic factors and the walk-run gait transition speed during human locomotion. *J. Appl. Biomech.* 24 (2008), 149–157.
- [21] KUO, A. D. The relative roles of feedforward and feedback in the control of rhythmic movements. *Motor Control* 6 (2002), 129–145.
- [22] LEE, J. *Vehicle Inertia Impact on Fuel Consumption of Conventional and Hybrid Electric Vehicles Using Acceleration and Coast Driving Strategy*. PhD thesis, Virginia Polytechnic Institute and State University, 2009.
- [23] LIEBENBERG, L. Persistence hunting by modern hunter-gatherers. *Curr. Anthropol.* 47 (2006), 1017–1025.
- [24] MAFFELS, C., SCHUTZ Y, Y., SCHENA, F., ZAFFANELLO, M., AND PINELLI, L. Energy expenditure during walking and running in obese and nonobese prepubertal children. *J. Pediatrics* 123, 2 (1993), 193–199.
- [25] MARGARIA, R. *Biomechanics and Energetics of Muscular Exercise*. Oxford, UK, Clarendon Press., 1976.
- [26] MELBY, C., SCHOLL, C., EDWARDS, G., AND BULLOUGH, R. Effect of acute resistance exercise on postexercise energy expenditure and resting metabolic rate. *J Appl Physiol.* 75 (1993), 1847–1853.

- [27] MERCIER, J., GALLAIS, D. L., M. DURAND, C. G., MICALLEF, J. P., AND PRÉFAUT, C. Energy expenditure and cardiorespiratory responses at the transition between walking and running. *Eur. J Appl. Physiol. and Occup. Physiol.* 69 (1994), 525–529.
- [28] MINETTI, A., AND ALEXANDER, R. M. A theory of metabolic costs for bipedal gaits. *J. Theor. Biol* 186 (1997), 467–476.
- [29] MINETTI, A. E., ARDIGO, L. P., AND SAIBENE, F. The transition between walking and running in humans: metabolic and mechanical aspects at different gradients. *Acta Physiol. Scand.* 150 (1994), 315–323.
- [30] MOHLER, B. J., THOMPSON, W. B., CREEM-REGEHR, S. H., PICK, H. L., AND WARREN, W. H. Visual flow influences gait transition speed and preferred walking speed. *Exp. Brain Res.* 181 (2007), 221228.
- [31] NEPTUNE, R. R., AND SASAKI, K. Ankle plantar flexor force production is an important determinant of the preferred walk-to-run transition speed. *J. Exp. Biol.* 208 (2005), 799–808.
- [32] NOBLE, B., METZ, K., PANDOLF, K. B., BELL, C. W., CAFARELLI, E., AND SIME, W. E. Perceived exertion during walking and running. ii. *Med. Sci. Sports* 5 (1973), 116–120.
- [33] PENNYCUICK, C. J. On the running of the gnu *connochaetes taurinus* and other animals. *J. Exp. Biol.* 63 (1975), 775–799.
- [34] PONTZER, H. Predicting the energy cost of terrestrial locomotion: a test of the limb model in humans and quadrupeds. *J. Exp. Biol.* 210 (2007), 484–494.
- [35] PRILUTSKY, B. I., AND GREGOR, R. J. Swing- and support-related muscle actions differentially trigger human walk-run and run-walk transitions. *J. Exp. Biol.* 204 (2001), 2277–2287.
- [36] RAYNOR, A. J., YI, C. J., ABERNETHY, B., AND JONG, Q. J. Are transitions in human gait determined by mechanical, kinetic or energetic factors? *Hum Movement Sci* 21 (2002), 785–805.
- [37] RUDIN, W. *Real and complex analysis*. McGraw-Hill, 1987.
- [38] SALVO, V. D., BARON, R., TSCHAN, H., MONTERO, F. J. C., BACHL, N., AND PIGOZZI, F. Performance characteristics according to playing position in elite soccer. *Int J Sports Med* 28 (2007), 222227.
- [39] SCHMIDT-NIELSEN, K. Locomotion: Energy cost of swimming, flying, and running. *Science* 177 (1972), 222–228.
- [40] SRINIVASAN, M. Optimal speeds for walking and running, and walking on a moving walkway. *CHAOS* 19 (2009), 026112.
- [41] SRINIVASAN, M. Fifteen observations on the structure of energy minimizing gaits in many simple biped models. *J Roy Society Interface* 8 (2011), 74–98.
- [42] SRINIVASAN, M., AND RUINA, A. Computer optimization of a minimal biped model discovers walking and running. *Nature* 439 (2006), 72–75.
- [43] STEUDEL-NUMBERS, K. L., AND WALL-SCHEFFLER, C. M. Optimal running speed and the evolution of hominin hunting strategies. *J. Human Evol.* 56 (2009), 355–360.
- [44] TERBLANCHE, E., CLOETE, W. A., DU PLESSIS, P. A. L., SADIE, J. N., STRAUSS, A., AND UNGER, M. The metabolic transition speed between backward walking and running. *Eur. J. Appl. Physiol.* 90 (2003), 520–525.
- [45] THORSTENSSON, A., AND ROBERTSON, H. Adaptations to changing speed in human locomotion: speed of transition between walking and running. *Acta. Physiol. Scand.* 131 (1987), 211–214.
- [46] TSEH, W., BENNETT, J., CAPUTO, J. L., AND MORGAN, D. W. Comparison between preferred and energetically optimal transition speeds in adolescents. *Eur J Appl Physiol* 88 (2002), 117–121.
- [47] USHERWOOD, J. R. Why not walk faster? *Biol. Lett.* 1 (2005), 338341.
- [48] USHERWOOD, J. R., AND BERTRAM, J. E. A. Gait transition cost in humans. *Eur J. Appl. Physiol.* 90 (2003), 647–650.
- [49] VAN INGEN SCHENAU, G. J. Some fundamental aspects of the biomechanics of overground versus treadmill locomotion. *Medi. Sci. Sports Exer.* 12 (1980), 257–261.

- [50] WALT, W. H. V. D., AND WYNDHAM, C. H. An equation for prediction of energy expenditure of walking and running. *J. Appl Physiol* 34, 5 (1973).
- [51] WARD-SMITH, A. J. Aerodynamic and energetic considerations relating to undulating and bounding flight in birds. *J. theor. Biol.* 111 (1984), 407–417.
- [52] WEINSTEIN, R. B., AND FULL, R. J. Intermittent locomotion increases endurance in a gecko. *Physiol Biochem Zool* 72 (1999), 732–739.
- [53] WILLIAMS, T. M. Intermittent swimming by mammals: A strategy for increasing energetic efficiency during diving. *Amer. Zool.* 41 (2001), 166–176.

Supporting Information Appendix to
“Walking, running and resting under time, distance and average
speed constraints: Optimality of walk-run-rest mixtures”

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This *Supporting Information* appendix has the following pieces.

1. **Section S1. Optimality of mixture strategies arising from ‘non-convexity.’** This section describes in greater mathematical detail why non-convexity of cost curves result in mixture strategies, and proving the results for a more general optimization problem allowing arbitrary speed changes. Supports sections 3.2-3.5 of the primary manuscript.
2. **Section S2. Effect of transient costs: Overground locomotion (Numerical Optimization).** This section describes in greater detail the mathematical formulation and the numerical optimization methods for the energy minimization calculation corresponding to overground locomotion including costs for transients. Supports section 3.6 of the primary manuscript.
3. **Section S3. Treadmill locomotion: Long versus short treadmills (Numerical Optimization).** This section describes in greater detail the mathematical formulation and the numerical optimization methods for the energy minimization calculation corresponding to treadmill locomotion, for finite treadmill sizes. Supports section 3.7 of the primary manuscript.
4. **Section S4. Further experimental details and observations.** This section discusses more technical information about the experimental protocol, including measurement accuracy, data processing procedures, and some discussion. Supports *Material and Methods* and section 2 of the primary manuscript.
5. **Section S5. Why more behavioral variability near the transition.** This section contains the mathematics for a brief remark made in the primary manuscript (section 4.2) about the relation between the observed variability in gait fractions and the slope of the mean gait fraction curve.
6. **Figure S5.** Provides the geometric proof of a paragraph (section 5.4) of the primary manuscript: “walk faster if you can lie down at the end.”

S1 Optimality of mixture strategies arising from ‘non-convexity’

On account of its potential broader applicability to human and animal behavior, we discuss the basic mathematics involved in the optimality of “mixture strategies” (such as walk-run mixtures) in an abstract setting. We then consider the special case of using walk-run or walk-stand mixtures in time-constrained locomotion. More sophisticated discussions are implicit in various math and physics texts on convex analysis and phase transitions. e.g., [1, 8, 7]. For simplicity, we assume that the functions involved are sufficiently well-behaved so that we may dispense with specifying the general smoothness conditions under which the following claims are true. We also only consider strict inequalities, ignoring the difference between convex and strictly convex.

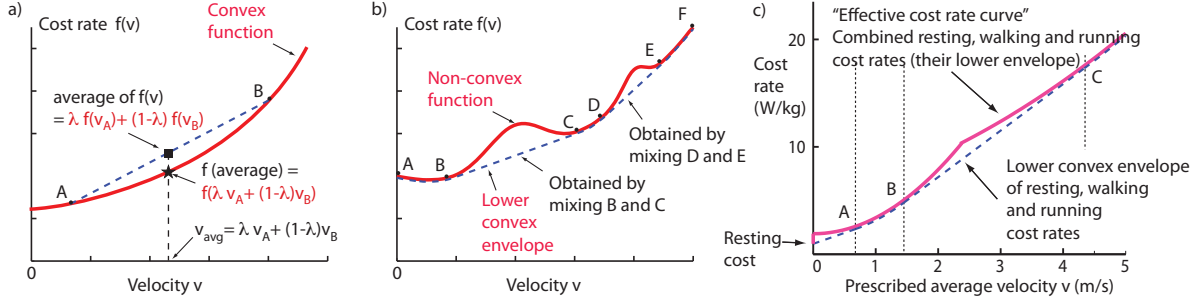


Figure S1: a) A convex function is shown (solid red line). A strictly convex function is one for which the straight line joining any two points on it is strictly above that function. b) A non-convex function (solid red line) and its lower convex envelope (dotted line) are shown. The straight line BC (DE) is a lower tangent to the function, touching it at two points of tangency B and C (D and E). c) We apply the ideas in panel-b to the combined ‘effective cost curve’ obtained for resting, walking, and running (solid pink line). The lower convex envelope (dotted line) deviates from the cost function at really slow average speeds (below A) when a walk-rest mixture is optimal and at intermediate speeds (between B and C) when a walk-run mixture is optimal. From A to B, pure walking is optimal and to the right of C, pure running is optimal.

Convex functions. Colloquially, a function $f(v)$ is called convex if it is, in a general sense, ‘bowl-shaped.’ Here, we identify the scalar function $f(v)$ with the energy or cost rate, and the scalar variable v with forward speed, but the following considerations are independent of such identification. A strictly convex function (as shown in Figure S1a) is such that any line connecting two points A and B on it, will lie entirely above the function between A and B. This statement can be written in terms of weighted averages (also called ‘convex combinations’) as follows.

The weighted average of velocities v_A and v_B is $v_{\text{avg}} = \lambda v_A + (1 - \lambda)v_B$. We use $0 < \lambda < 1$, so that $v_A < v_{\text{avg}} < v_B$. Convexity implies that the function value at this weighted average $f(v_{\text{avg}})$ is always below the weighted average of the function values $f(v_A)$ and $f(v_B)$:

$$f(\lambda v_A + (1 - \lambda)v_B) < \lambda f(v_A) + (1 - \lambda)f(v_B). \quad (\text{S1})$$

In Figure S1a, the left hand side of the above inequality is the point on the convex function denoted by a five-pointed star and the right hand side is the corresponding point on the straight line between A and B denoted by a square.

Non-convex functions. Non-convex functions have some regions where the inequality Eq. S1 is reversed. For instance, the non-convex function shown in Figure S1b is such that between B and C, the function value is above the straight line joining B and C. That is,

$$f(\lambda v_B + (1 - \lambda)v_C) > \lambda f(v_B) + (1 - \lambda)f(v_C). \quad (\text{S2})$$

for $0 < \lambda < 1$. In other words, the value obtained by averaging $f(v_B)$ and $f(v_C)$ can be lower than $f(v_{\text{avg}})$.

Lower convex envelope. The lower convex envelope of a convex function (for instance, the function in Figure S1a) is the convex function itself. The lower convex envelope of a non-convex function is constructed as follows. For each v , first consider the tangent to the function $f(v)$. For v such that the tangent is entirely

below the whole function (except for the point of tangency), such as in the intervals A to B, C to D, and E to F in Figure S1b, the lower convex envelope is equal to the function $f(v)$. But then, in the other regions, for instance from B to C and D to E, the non-convex function is replaced by a tangent to the function that touches it (tangentially) at two points. B, C, D, and E are points of tangency of these supporting tangents (shown as dashed lines). Thus the lower convex envelope of the non-convex function in Figure S1b is the dashed curve consisting of straight-line parts and curved parts. To give a physical analogy, the lower convex envelope is the curve traced by a taut flexible string ‘supporting the non-convex function’ from below.

Lower convex envelope is the optimal attainable by averaging. It turns out that the lower convex envelope of a function is the *lowest function value one can get by taking the weighted average* of any two points on the curve, for a given weighted average v_{avg} . In other words, if we wish to find v_1 , v_2 and λ such that the weighted average $g = \lambda f(v_1) + (1 - \lambda)f(v_2)$ is minimized, constrained by $v_{\text{avg}} = \lambda v_1 + (1 - \lambda)v_2$, then the function that we get as a function of v_{avg} is the lower convex envelope. The construction of the lower convex envelope in the previous paragraph essentially replaces the function value $f(v)$ with the lowest value obtainable by taking averages of function values at other points. Stated differently, the lower supporting tangents, such as BC and DE are the lowest chords we can get while still touching the function at two points.

Application to the locomotion energy curves. With only a little modification, the above analysis can be applied to the optimization problem involving a choice between walking, running, and resting. First, we replace the three different energy rates, the resting energy rate e_{rest} (defined only at $v = 0$), the walking energy rate $\dot{E}_w(v)$ and the running energy rate $\dot{E}_r(v)$ by a single function $f(v)$ defined as the lower among the three costs at each applicable velocity. This function $f(v)$, called the ‘lower envelope’ (the ‘effective cost curve’ of the primary manuscript) as opposed to the ‘lower convex envelope,’ is shown as a solid pink line in Figure S1c. This $f(v)$ curve is the best attainable cost for ‘pure strategies.’ Notice that this function $f(v)$ is not convex. Therefore, if we allow weighted mixtures of two gaits and/or speeds, the lower convex envelope (shown as a dotted line in Figure S1c) of the lower envelope $f(v)$ is the best attainable cost rate. As discussed in the main text, at low v to the left of A, we see that a walk-rest mixture is best, and between B and C, a walk-run mixture is optimal. Between A and B, the lower convex envelope hugs the walking cost curve, so pure walking is optimal. Beyond C, the lower convex envelope hugs the running cost curve, so pure running is optimal.

This completes our discussion of the optimal locomotion strategies in Figure 3 and 4 of the main article.

Can we do better by averaging more than two points? No. It turns out that the best reduction in average value is obtained by mixing at most two points on $f(v)$.

The proof of this claim uses a generalized version of the inequality in Eq. S1, called Jensen’s inequality [1, 5]. For a strictly convex function $f(v)$, if we consider using a mixture of finitely many v_i , we have:

$$f(\lambda_1 v_1 + \lambda_2 v_2 + \lambda_3 v_3 + \dots) < \lambda_1 f(v_1) + \lambda_2 f(v_2) + \lambda_3 f(v_3) + \dots \quad (\text{S3})$$

where $\lambda_1 + \lambda_2 + \lambda_3 + \dots = 1$. Even more generally, for a continuously or discontinuously changing velocity function $v(t)$ (‘measurable’ $v(t)$ [5]) with some average v_{avg} and for a strictly convex function $f(v)$:

$$\underbrace{f(v_{\text{avg}})}_{\text{function at the average}} < \underbrace{\frac{1}{T} \int_0^T f(v(t)) dt}_{\text{average of the function}} \quad \text{given an average } v \text{ constraint } \frac{1}{T} \int_0^T v(t) dt = v_{\text{avg}}. \quad (\text{S4})$$

These inequalities essentially say that if we have a convex cost rate, we cannot lower it by averaging over two, three, or infinitely many points. Observing that the ‘lower convex envelope,’ obtained by averaging at most two points, is already convex, we cannot lower it any further by averaging two or more points on it. Thus, the best attainable average cost rate at a given v_{avg} is given by the lower convex envelope.

S2 Effect of transient costs: Overground locomotion (Numerical Optimization)

In this section, we discuss the methods we used to obtain Figure 5a of the main manuscript, in which we display the optimal transitions in the presence of costs for transients.

First, consider two extremes: (1) when the transition costs are large enough, any transition in speed or gait will be disfavored, so it would be optimal to walk all the way or run all the way at constant speed equal to the prescribed average; (2) when the transition costs are negligible, the optimal strategies approach that discussed above in section S1 and in Figures 3-4 of the main article. Below, we consider situations between these two extremes; we may expect optimal mixture strategies when the increased cost due to a transient is more than made up by a cost reduction due to using a mixture.

Optimal gaits with transient costs: a numerical optimization solution. We now discuss the problem of traveling a finite distance overground, in a given amount of time, while minimizing the total metabolic energy cost, with a cost for any velocity transients. In particular, we consider locomotion strategies of the form Figure S2a, with exactly resting phase, walking phase, and running phase. The velocity starts at zero and ends at zero.

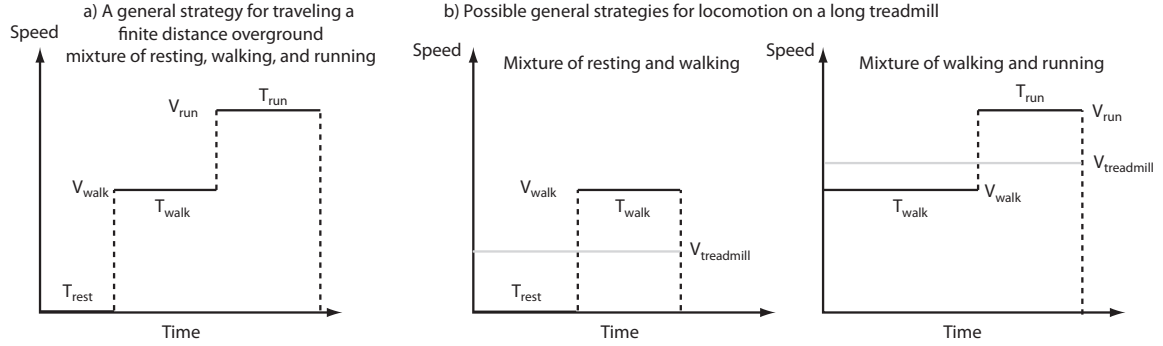


Figure S2: Space of locomotion strategies considered for the numerical optimization problems. a) Overground locomotion for a finite distance. We consider strategies that, most generally, use a mixture of walking, running and resting (exactly one phase each), with the possibility of the various special cases. b) Locomotion on a bounded treadmill. We consider two possible general strategies: a walk-rest mixture and a walk-run mixture, along with their various special cases.

The unknowns of the optimization problem are T_{rest} , T_{walk} , T_{run} , V_{walk} , and V_{run} , as seen in Figure S2a. In addition to the metabolic rates corresponding to resting, walking, and running, we have a cost for changes in velocities, proportional to the positive or negative work performed in the transition, equal to the changes in kinetic energy (again, mass-normalized):

$$\text{Increases in kinetic energy} = \text{Decreases in kinetic energy} = \left(\frac{1}{2} V_{\text{run}}^2 - \frac{1}{2} V_{\text{walk}}^2 \right) + \left(\frac{1}{2} V_{\text{walk}}^2 - 0 \right) = \frac{1}{2} V_{\text{run}}^2. \quad (\text{S5})$$

Thus, the total cost of the journey is:

$$E_{\text{total}} = \underbrace{\dot{E}_{\text{rest}} T_{\text{rest}} + \dot{E}_{\text{walk}} (V_{\text{walk}}) T_{\text{walk}} + \dot{E}_{\text{run}} (V_{\text{run}}) T_{\text{run}}}_{\text{cost for steady state locomotion and resting}} + \underbrace{(b_1 + b_2) \frac{1}{2} V_{\text{run}}^2}_{\text{total transition cost}}. \quad (\text{S6})$$

The scaling coefficients $b_1 = 4$ and $b_2 = 1.2$ are the reciprocals of the muscle efficiencies for performing positive and negative work [3, 6]. The usual total time and total distance constraints hold:

$$\begin{aligned} T_{\text{rest}} + T_{\text{walk}} + T_{\text{run}} &= T_{\text{allowed}} & (\text{S7}) \\ \text{and } V_{\text{walk}} T_{\text{walk}} + V_{\text{run}} T_{\text{run}} &= D_{\text{required}}. & (\text{S8}) \end{aligned}$$

In addition, we have some natural inequality constraints:

$$V_{\text{walk}}, V_{\text{run}} \geq 0 \quad (\text{S9})$$

$$\text{and } V_{\text{walk}} \leq V_{\text{run}}. \quad (\text{S10})$$

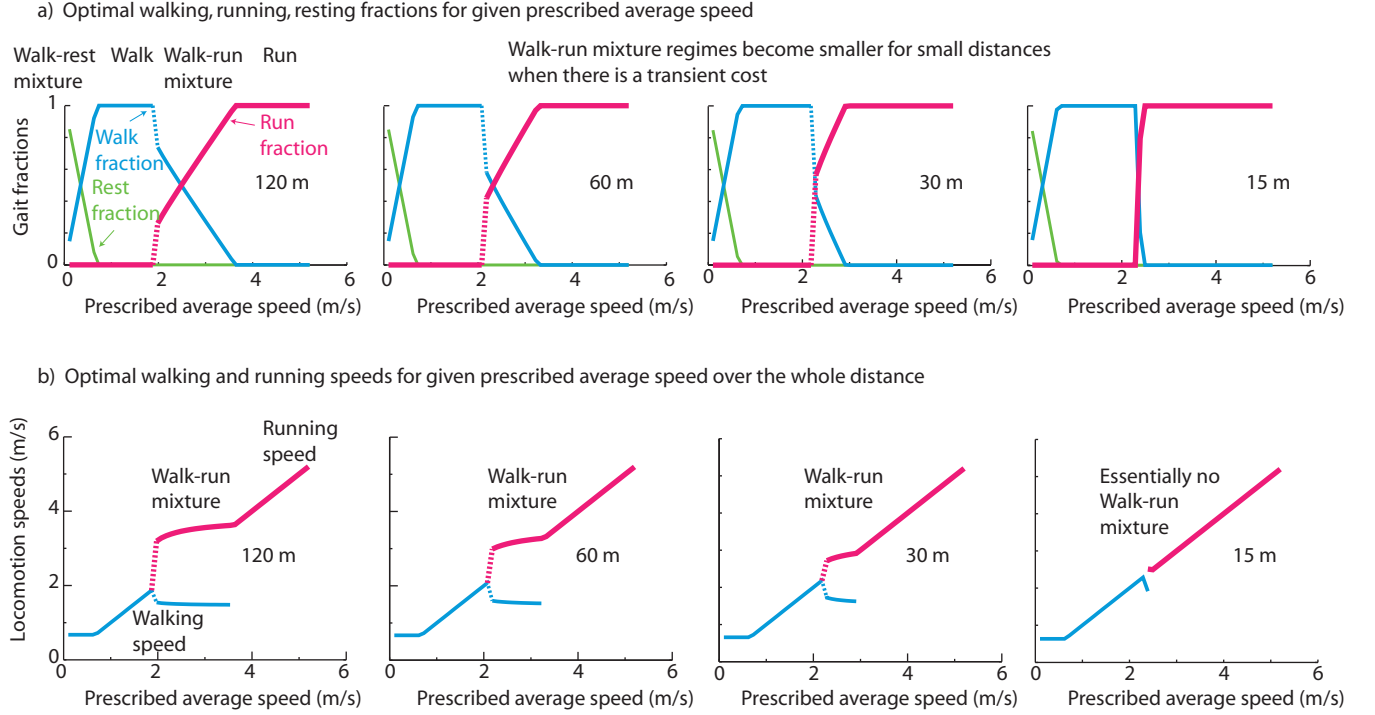


Figure S3: Optimal walk-run-rest strategies for overground locomotion in the presence of transient costs, when traveling a finite distance (distances considered: 120 m, 60 m, 30 m and 15 m). a) Optimal fractions of resting, walking, and running are shown as a function of prescribed average speed, for different total distances. Notice that the speed regime in which a walk-run mixture is optimal shrinks for shorter distances. b) The optimal walking and running speeds to be used are shown. Notice that in the walk-run mixture regime, the walking speed is lower than the running speed; the difference between these two speeds decreases as the total distance decreases.

The above mathematical optimization problem requires the minimization of nonlinear functions of a few variables, subject to a mixture of equality and inequality constraints, both linear and nonlinear. Such optimization problems are called “nonlinear programming” problems. Local minima to such problems may be obtained reliably using nonlinear programming software using methods such as ‘sequential quadratic programming,’ for instance, as implemented in SNOPT or NPSOL [2, 4].

The general locomotion strategy we have assumed, involving a mixture of resting, walking, and running (Figure S2a), can retrieve as special cases all of the following strategies: rest-walk mixture, pure walking, walk-run mixture, and pure running, without any loss of generality. More significantly, the special cases are obtained with no extra cost penalty as follows. Optimal rest-walk is obtained by $T_{\text{run}} = 0$ and $V_{\text{run}} = V_{\text{walk}}$. Optimal pure walking is obtained by $T_{\text{rest}} = 0$, $T_{\text{run}} = 0$, and $V_{\text{run}} = V_{\text{walk}}$. Optimal walk-run is obtained by $T_{\text{rest}} = 0$. Optimal pure running is obtained by $T_{\text{rest}} = 0$, $T_{\text{walk}} = 0$, and $V_{\text{run}} \geq V_{\text{walk}}$.

We used the optimization program SNOPT [2] to solve this optimization problem (see [7] for some more details on such optimization problems). We solved the problem for four different distances $D_{\text{required}} = 120$ m, 60 m, 30 m, 15 m. For each of these distances, we considered 50 different T_{allowed} , corresponding to prescribed average speeds between 0.1 and 5.2 m/s. We solved for the optimal solution for each of these $D_{\text{required}}-T_{\text{allowed}}$ combinations. The optimal strategy as a function of the prescribed average speed is shown in Figure S3a-b. For each of these optimization problems, we used about 50 initial seeds for the optimization; if the optimization converged to apparently different local minima, we pick the optimum with the least cost at a given $D_{\text{required}}-T_{\text{allowed}}$ combination (essentially assuring that we found the global optimum, given the simplicity of the problem).

Qualitatively, the optimal solutions are as we would expect. When the total distance is large-enough, the qualitative features of the optimal strategies are essentially identical to the case when no transient cost was considered (Figures 3-4 of the main article). This is because over long distances, the transient costs become negligible compared to the steady state costs integrated over the whole time. When the distance becomes smaller, the differences with the no-transient-cost case become apparent:

1. The walk-run mixture regime becomes smaller and smaller as the distance becomes smaller, essentially vanishing at 15 m. This is because the transient cost (which is a one-time cost) becomes substantial compared to the benefit derived from using a mixture (which scales with distance traveled). The effect of the transition cost is less on the walk-rest mixture regime as the transition cost due to kinetic energy of walking is smaller.
2. During walk-run mixtures, the walking speed is lower than the running speed. But the difference between the walking and running speeds used in these walk-run mixtures decreases as the total distance reduces (because too high a speed difference entails too high a transition cost).
3. There appears to be a discontinuous reduction in the walking speed when we go from a pure-walk regime to the walk-run regime. This discontinuity is due to a non-zero transient cost; the discontinuity decreases to zero if the proportionality constant on the transient cost ($b_1 + b_2$) is taken to zero.

S3 Treadmill locomotion: Long versus short treadmills (Numerical Optimization)

When a treadmill is very short, as most treadmills are in the real world, walk-run mixtures are unlikely to provide large energy benefits (without fatigue mechanisms), because of the costs of switching gaits or switching speeds. But if the treadmill is very long and the task is to stay on the treadmill, the optimal strategies at various treadmill speeds will be just as discussed in the main article (Figure 3a-b), because in this limit, the transition costs will become negligible compared to steady state costs.

To explore the effect of bounded treadmill size, we solved numerical optimization problems analogous to those solved in the previous section (section S2), but adapted to the treadmill context. The treadmill context is different from the overground context in three key ways:

1. For treadmill locomotion, there is no explicit time constraint, but only that the person remains on the treadmill. So the speed and gait of the subject is assumed to be periodic with some unknown period T_{period} , repeating forever. Walking or running at constant speed is a special case, as are walk-run and walk-rest mixtures. For a walk-run mixture, the subject would alternate periodically between walking and running.
2. The subject’s velocity fluctuations should be such that her position can never lie outside the extent of the treadmill. That is, the subject has a “position constraint.”
3. The task is simply remain on the treadmill (and not necessarily get anywhere). Thus, the energy cost to be minimized would be the average metabolic rate over a long period of time: $E_{\text{period}}/T_{\text{period}}$.

Say the constant treadmill speed is V_{avg} ; we use this notation because V_{avg} will also be the average speed of the subject over a period. The treadmill length is D . The subject is assumed to remain on the treadmill if her fore-aft position x satisfies $0 \leq x \leq D$.

Optimizing among walk-rest strategies. We consider two distinct general strategies from which to find an optimal strategy: a periodic walk-rest strategy shown in Figure S2b and a periodic walk-run strategy shown in Figure S2c. First, we consider walk-rest strategies.

For optimizing over walk-rest strategies (see Figure S2b), the unknowns are T_{rest} , T_{walk} , and V_{walk} , and in addition, the initial position of the subject x_0 along the treadmill ($0 \leq x_0 \leq D$). Here, the unknown speed V_{walk} is relative to the treadmill, so that the speed relative to the ground will be $V_{\text{walk}} - V_{\text{avg}}$ when walking (and $0 - V_{\text{avg}}$ when resting). The subject’s position $x(t)$ relative to the ground as a function of time t is then given by:

$$x(t) = x_0 + (0 - V_{\text{avg}})t \text{ for } 0 \leq t \leq T_{\text{rest}}, \quad (\text{S11})$$

$$x(t) = x_0 - V_{\text{avg}} T_{\text{rest}} + (V_{\text{walk}} - V_{\text{avg}}) (t - T_{\text{rest}}) \text{ for } T_{\text{rest}} \leq t \leq T_{\text{rest}} + T_{\text{walk}}. \quad (\text{S12})$$

Because we have assumed that the subject’s motion is periodic, the subject’s position must return to x_0 at the end of one period $T_{\text{period}} = T_{\text{rest}} + T_{\text{walk}}$:

$$x_0 - V_{\text{avg}} T_{\text{rest}} + (V_{\text{walk}} - V_{\text{avg}}) T_{\text{walk}} = x_0.$$

The constraint of remaining on the treadmill for all time reduces to:

$$0 \leq x(t) \leq D \text{ for } 0 \leq t \leq T_{\text{period}},$$

where $T_{\text{period}} = T_{\text{rest}} + T_{\text{walk}}$. We convert this continuous-time constraint into finitely many constraints by enforcing the inequality at a few salient times (see [7]).

The total energy cost to be minimized is the average metabolic energy rate over one period:

$$\dot{E}_{\text{avg}} = \frac{e_{\text{rest}}T_{\text{rest}} + \dot{E}_{\text{walk}}(V_{\text{walk}})T_{\text{walk}} + 0.5(b_1 + b_2)V_{\text{walk}}^2}{T_{\text{period}}}.$$

In the above cost expression, the $0.5(b_1 + b_2)V_{\text{walk}}^2$ term is due to the work done during transients.

We now have a nonlinear programming problem, as before. Note that the walk-rest strategies can give rise to pure walking as a special case with $T_{\text{rest}} = 0$ and $T_{\text{walk}} > 0$.

Optimizing among walk-run strategies. For a walk-run strategy, the unknowns are T_{walk} , T_{run} , V_{walk} , and V_{run} , and the initial position of the subject x_0 along the treadmill ($0 \leq x_0 \leq D$). The subject's position relative to the ground as a function of time t is then given by:

$$x(t) = x_0 + (V_{\text{walk}} - V_{\text{avg}})t \text{ for } 0 \leq t \leq T_{\text{walk}}, \quad (\text{S13})$$

$$x(t) = x_0 + (V_{\text{walk}} - V_{\text{avg}})T_{\text{walk}} + (V_{\text{run}} - V_{\text{avg}})(t - T_{\text{walk}}) \text{ for } T_{\text{walk}} \leq t \leq T_{\text{walk}} + T_{\text{run}}. \quad (\text{S14})$$

The subject's periodicity requires that the subject's position return to x_0 at the end of one period $T_{\text{period}} = T_{\text{walk}} + T_{\text{run}}$:

$$x_0 + (V_{\text{walk}} - V_{\text{avg}})T_{\text{walk}} + (V_{\text{run}} - V_{\text{avg}})T_{\text{run}} = x_0.$$

The constraint of remaining on the treadmill for all time reduces to:

$$0 \leq x(t) \leq D \text{ for } 0 \leq t \leq T_{\text{period}},$$

where $T_{\text{period}} = T_{\text{walk}} + T_{\text{run}}$. The total energy cost to be minimized is:

$$\dot{E}_{\text{avg}} = \frac{\dot{E}_{\text{walk}}(V_{\text{walk}})T_{\text{walk}} + \dot{E}_{\text{run}}(V_{\text{run}})T_{\text{run}} + 0.5(b_1 + b_2)(V_{\text{run}}^2 - V_{\text{walk}}^2)}{T_{\text{period}}}.$$

In the above cost expression, the term $0.5(b_1 + b_2)(V_{\text{run}}^2 - V_{\text{walk}}^2)$ is due to the work done during transients. Again, we have a nonlinear programming problem. Note that these walk-run strategies can give rise to both pure walking ($T_{\text{walk}} = 0$ and $V_{\text{walk}} = V_{\text{run}}$) and pure running ($T_{\text{run}} = 0$ and $V_{\text{walk}} = V_{\text{run}}$) as special cases.

Optimal solution and results. We solve the optimization problems using SNOPT [2], for given treadmill length D and treadmill speed V_{avg} . We consider five different treadmill lengths $D = 40$ m, 10 m, and 1 m. At each of these treadmill lengths, we solved both the walk-rest optimization problem and the walk-run optimization problem for a range of treadmill speeds from 0.1 m/s to 5.2 m/s. For each of these optimizations, we started from about 20 random initial seeds to increase the chances of finding the global optimum. For each D and V_{avg} , we declare the converged solution with the lowest cost as the putative global optimal strategy.

Figure S4 shows the result of the numerical optimizations for different treadmill lengths. As usual, there are four regimes, a walk-rest regime, a pure constant-speed walking regime, a walk-run regime, and a pure constant-speed running regime.

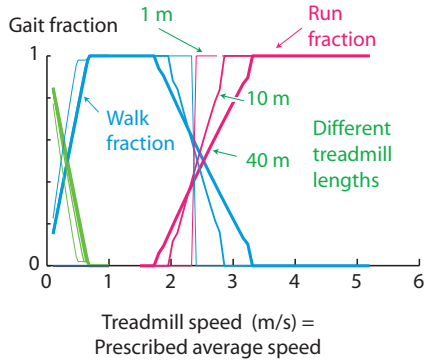
During a walk-run mixture, the subject runs faster than the treadmill, so moves forward relative to the ground, and then walks slower than the treadmill, moving backward relative to the ground. Figure S4a shows that for walk-run mixture regime is larger for the 40 m treadmill, and is essentially non-existent for a 1m treadmill. The difference in the walking and running speeds in the optimal walk-run mixtures decreases to zero as the treadmill length decreases, as seen in Figure S4b.

During a walk-rest mixture, the subject walks faster than the treadmill, traveling forward relative to the ground, and then rests, traveling toward the back of the treadmill. The time period of either a walk-run or a walk-rest mixture is determined by the length of the treadmill.

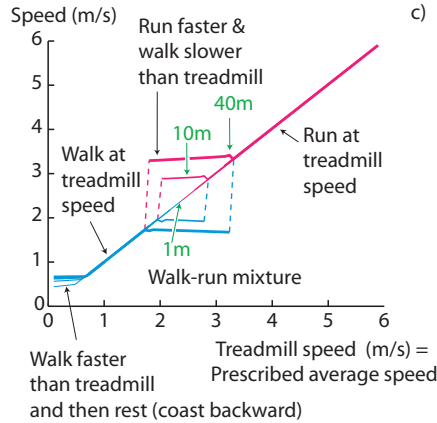
We suggest that experiments verifying these predictions be performed on airport moving walkways, whose speeds can be changed continuously (unfortunately, many moving walkways have a fixed gearbox with no simple provision for changing speeds).

Locomotion on a treadmill of finite length

a) Optimal fractions of resting, walking, running



b) Optimal walking and running speeds



c)

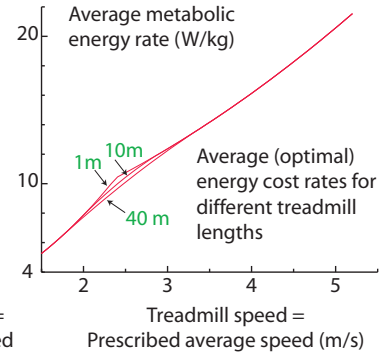


Figure S4: Optimal walk-run-rest strategies for locomotion on a treadmill with finite length. a) The resting, walking, and running fractions for three different treadmill lengths are shown, as a function of the constant treadmill speed. The 40 m treadmill is depicted with the thickest lines, and has the broadest regimes in which a walk-run mixture is optimal; the 1 m treadmill, depicted with the thinnest lines, has a sharp transition between walking and running, with a vanishing walk-run mixture regime. The walk-run transition regime becomes smaller with treadmill length. b) The optimal walking and running speeds to be used on treadmills of different lengths. Outside of the mixture-regimes, it is optimal to walk or run at exactly the treadmill speed. In the walk-run mixture regime, the running speed is higher and the walking speed is lower than the treadmill speed; the separation between walking and running speeds in the transition regimes becomes smaller as the treadmill becomes smaller. c) The average metabolic energy rate as a function of treadmill speed, for different treadmill lengths. For 40 m treadmills, because the subject can do a mixture of walking and running, with comparatively little transition cost, the optimal energy rate is close to the lower convex envelope of the cost curves. For the 1 m treadmills, the subject essentially walks or runs at the treadmill speed, so the average metabolic rate follows the individual cost curves more closely.

S4 Further experimental details and observations

Video-based running fractions. Independent counts of running fractions by the two researchers watching videos of the experimental trials produced the same numbers typically to about a second. When the choice was between walking and running, the walking fraction includes any left-over time if the subject arrived early to her destination or, essentially equivalently, slowed down dramatically before the destination. Thus, effectively, the subject can only arrive late. No systematic differences were seen when the equivalent of Figure 1 in the main article was plotted for men versus women, or the top 25 percentile of leg length versus the bottom 25 percentile.

Speed measurements. The speed measurements displayed in Figure 2a-b of the main article are from a high-end Global Positioning System (GPS) device VBOX MINI (Racelogic UK). The speed is reported at 10 Hz and the GPS device's documentation claims an accuracy of 0.03 m/s when 4 consecutive samples are averaged. Even if this was an underestimation by a factor of 5, the resulting accuracy would be sufficient for the claims made in the article, in which we try to discriminate speed peaks that are separated by about 1 m/s. The GPS device weighs less than 900 grams and was worn by the subjects at their hip in a light utility belt. The subjects wore a light bike helmet with an external GPS antenna. These GPS subjects' behavior was not different from the rest.

Ten outdoor subjects performed our basic protocol experiments with this GPS device. The rest of the subjects did not have this device on them. No filtering or smoothing of the GPS derived speed was performed in the creation of Figure 2a-b of the main article. As noted in Figure 2b, not all subjects had a two-peaked speed profile. While 10 subjects and 15 speeds implies 150 trials, for Figure 2a we dropped 10 trials for which the GPS data was either missing or the GPS derived average speed was more than 0.2 m/s from the prescribed average speed. The double peaked speed profile for individual subjects, when they did have it, were much sharper and distinct than is evident in the pooled histogram of Figure 2a of the main article. That

this broadening of peaks is inevitable is apparent from considering the speed plateaus in Figure 2b of the main article; in particular, note that the walking speed plateaus of the subjects 4–6 are slightly different. A further broadening of the peaks is on account of the noise-like fluctuations in the speed data, seen in Figure 2b. These fluctuations, which ‘seem’ noise-like over time-scale of 60 seconds, are partly due to natural speed fluctuations that the hip undergoes within a walking or running step: in walking, forward speed is minimum around mid-single-support and maximal around the step-to-step transition; in running, forward speed is also minimal during mid-single-support and is higher during flight phase.

Stride frequency measurements. Stride frequency measurements in Figure 2c of the main article were from ‘Garmin footpod’ and video-based counting. The footpod is an accelerometer-based step counter, weighs little more than a door key, and was attached to one of the shoes of the subject. Using calibration trials, we inferred that the readings reported by the footpod were accurate only as moving time-averaged results of the number of steps over about 15 seconds. While stride frequency errors in steady state could be very small, during transients, the error could be as high as 0.2 Hz. This means that the peaks in stride frequency were likely broader than could be inferred from a more accurate step counter, making the possible double peaks in the stride frequency histograms not very distinct. To mitigate some smoothening effects of the moving average, we used video recordings of the studies to correct the steps counts over the initial and final 20 seconds of each trial. Future studies would use more accurate accelerometers or foot switches for better time-resolution.

S5 Why more behavioral variability near the transition

We provide a brief mathematical comment on why variability might be related to the slope of the running fraction curve.

Say a subject had an ideal running fraction $\lambda_r(v)$ (whether it is energy-optimal or not) which the subject would use as a function of average speed in the absence of any ‘errors.’ But, say the subject uses the running fraction at an incorrect average speed $\bar{v} = v + \Delta v$, when traveling at v , the prescribed speed. Or, the subject travels at the incorrect speed \bar{v} , arriving earlier or later, while using the running fraction for the prescribed speed v . In both cases, we can derive an expression for the error in observed fraction $\bar{\lambda}_r$ as a function of prescribed speed v as follows:

$$\bar{\lambda}_r(v) = \lambda_r(v + \Delta v) \approx \lambda_r(v) + \frac{\partial \lambda_r}{\partial v} \cdot \Delta v \quad (\text{Taylor series}).$$

Therefore, for a given variance σ_v^2 for Δv , assuming zero mean ($\langle \Delta v \rangle = 0$), the variance σ_λ^2 in observed λ_r will be:

$$\sigma_\lambda^2 = \left(\frac{\partial \lambda_r}{\partial v} \right)^2 \cdot \sigma_v^2,$$

(using a standard result in basic probability theory) and therefore, the error standard deviation in observed running fraction is:

$$\sigma_\lambda = \left| \frac{\partial \lambda_r}{\partial v} \right| \cdot \sigma_v.$$

Exactly, the same mathematics and result applies when we are pooling multiple subjects, each with slightly different $\lambda_r(v)$, identical except for a shift sideways with some variance σ_v^2 .

Therefore, the variability in such pooled data from such subjects will be maximum at the transition regime, where the absolute slope $|\partial \lambda_r / \partial v|$ is maximal.

References

- [1] BOYD, S., AND VANDENBERGHE, L. *Convex Optimization*. Cambridge University Press, 2004.
- [2] GILL, P. E., MURRAY, W., AND SAUNDERS, M. A. SNOPT: An SQP algorithm for large-scale constrained optimization. *SIAM J. Optim.* 12 (2002), 979–1006.
- [3] MARGARIA, R. *Biomechanics and Energetics of Muscular Exercise*. Oxford, UK, Clarendon Press., 1976.
- [4] NOCEDAL, J., AND WRIGHT, S. J. *Numerical optimization*. Springer, 1999.

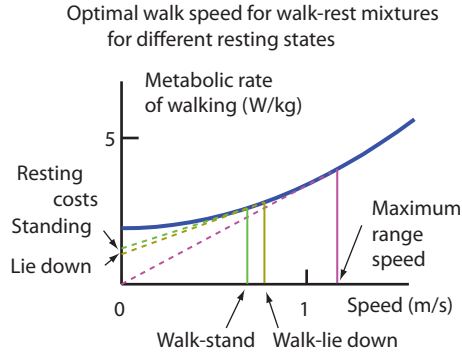


Figure S5: For different resting costs, the predicted walking speed in a walk-rest mixture is higher for lower resting cost. e.g., Walk faster if your resting state is sleeping rather than standing. Here, the lying down resting cost was simply picked to be smaller than the standing resting cost.

- [5] RUDIN, W. *Real and complex analysis*. McGraw-Hill, 1987.
- [6] RUINA, A., , BERTRAM, J. E. A., AND SRINIVASAN, M. A collisional model of the energetic cost of support work qualitatively explains leg-sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. *J. Theor. Biol.* 14 (2005), 170–192.
- [7] SRINIVASAN, M. Fifteen observations on the structure of energy minimizing gaits in many simple biped models. *Journal of the Royal Society Interface* 8 (2011), 74–98.
- [8] WALES, D. J. *Energy Landscapes*. Cambridge University Press, 2003.