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Contributions of metabolic and temporal costs to human gait selection

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Humans naturally select several parameters within a gait that correspond with minimizing metabolic cost. Much less is understood about the role of metabolic cost in selecting between gaits. Here, we asked participants to decide between walking or running out and back to different gait specific markers. The distance of the walking marker was adjusted after each decision to identify relative distances where individuals switched gait preferences. We found that neither minimizing solely metabolic energy nor minimizing solely movement time could predict how the group decided between gaits. Of our twenty participants, six behaved in a way that tended towards minimizing metabolic energy, while eight favoured strategies that tended more towards minimizing movement time. The remaining six participants could not be explained by minimizing a single cost. We provide evidence that humans consider not just a single movement cost, but instead a weighted combination of these conflicting costs with their relative contributions varying across participants. Individuals who placed a higher relative value on time ran faster than individuals who placed a higher relative value on metabolic energy. Sensitivity to temporal costs also explained variability in an individual's preferred velocity as a function of increasing running distance. Interestingly, these differences in velocity both within and across participants were absent in walking, possibly due to a steeper metabolic cost of transport curve. We conclude that metabolic cost plays an essential, but not exclusive role in gait decisions.

1. Introduction

Humans generally walk at slower speeds and run at faster speeds. In walking, metabolic cost when represented as a rate, increases nonlinearly as a function of velocity. Transforming metabolic rate to metabolic cost per distance, i.e. cost of transport (COT) [1] reveals a U-shaped curve with the minimum roughly corresponding to the preferred walking velocity of humans [2,3] and other animals [4,5] (figure 1*a*). In running, recent evidence suggests that metabolic rate also increases nonlinearly [7–10] and that this curved relationship, while much shallower than in walking, may influence how individuals select running velocity [6,11].

Metabolic cost has also been shown to play an important role in establishing how we select between gaits. When instructed to traverse fixed distances in a constrained time, humans allocated the relative time walking and running and the velocities at those gaits in a manner that minimized total metabolic energy expenditure [6]. When moving on a treadmill with increasing velocity, transitions between walking and running gaits tend to occur at velocities close to where the respective COT curves intersect [4,12,13], which for human walking and running is found at approximately 2.25 m s^{-1} (figure 1*a*) [12,13].

The metabolic cost of locomotion has also been shown to play an essential part in explaining how animals forage for food in their environment [14–17]. Recent models inspired by optimal foraging theory quantify the utility of each movement according to the interactions between minimizing the costs of the movement (both time and energy spent) and maximizing the benefits

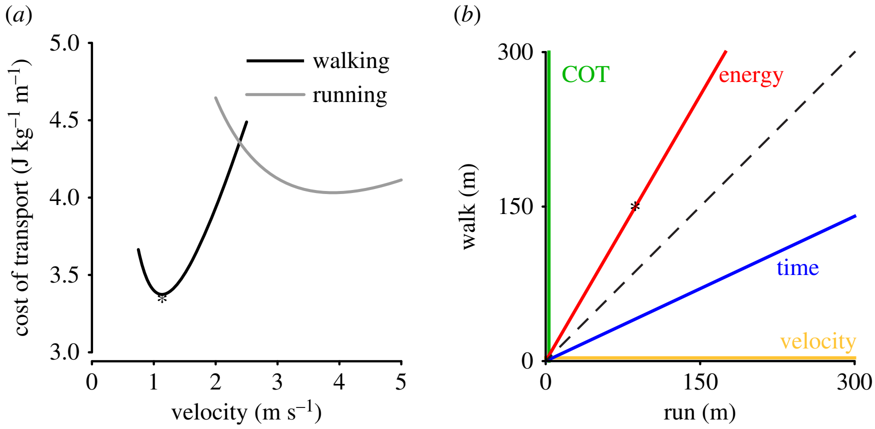

Figure 1. Model predictions. (*a*) Metabolic COT normalized by body weight for walking (black curve) and running (grey curve) using values reported in [6]. The asterisk (*) indicates that an individual minimizing COT would always choose to walk. (*b*) Model predictions for the slope of the indifference points. Dashed line represents unity. Minimizing COT predicts an individual would prefer to walk rather than run when allowed to choose their own velocities regardless of relative walking and running distances (green vertical line parallel vertical axis). The indifference line for minimizing total metabolic energy (red line) lies above unity suggesting that walking a greater distance carries an equal cost in terms of total metabolic energy as running a shorter distance. The indifference line for time (blue line) lies below unity suggesting that walking a shorter distance carries an equal cost in terms of time compared with running a longer distance. Walk/run combinations above model boundaries would predict a preference to run, whereas combinations below the line would predict a preference to walk. A model based on minimizing time per distance (maximizing velocity) would always predict that an individual would run regardless of relative distances (gold horizontal line). All predictions assume walking and running at constant, self-selected velocities where the walking velocity is slower than the running velocity. The asterisk represents a theoretical indifference point for an individual who minimizes total metabolic energy. For this individual, running 100 m and walking 150 m have equal utility.

of the movement outcome (primary and secondary reinforcers) [18,19]. An essential component of these models is that movements take time, which negatively influences utility [20]. This effect of time on movement utility is subjective, with certain individuals exhibiting a much greater sensitivity to temporal costs than other individuals [20].

We lack a clear understanding of how gait preferences are established when movement time is unconstrained. In this study, we attempted to understand how metabolic energy and time interact when choosing between walking and running gaits. We hypothesized that there would be situations in which running would be preferred over walking, despite the greater COT for running. Furthermore, we expected that preferences would best be explained using a utility model that does not exclusively minimize either metabolic cost or time, but instead would be based on a participant-specific combination of these two costs.

2. Methods

2.1. Theoretical development

We postulate that when an individual considers whether to walk or run, they behave in a way that maximizes movement utility (J), meaning they balance minimizing costs associated with each gait while maximizing reward as a result of successfully completing the trial. When deciding between performing different movements, the observed preference is assumed to be the option that carries greater utility. In the current paradigm, we assumed that changing the cumulative distance covered for a movement affected the utility of that movement. We introduce several candidate models to predict relative distances where the utility of each gait is equal to the other ($J_{\text{walk}} = J_{\text{run}}$) and then compare each model's predictions to the observed gait preference of each individual. We refer to the walking and running distances where participants switch preferences between gaits as 'indifference points'.

To emphasize the differences across candidate models, we represent indifference point predictions according to a linear function where the walking component of the indifference point (D_{w}) is predicted as a function of the running component (D_{r}) with the unity line of this space representing walk/run combinations of equal distance (figure 1*b*, dashed line). We refer to the slope of this linear function as the 'indifference slope'. Distance pairs falling above the indifference slope of each model predict a greater utility for running and combinations below the indifference slope predict a greater utility for walking. At no time during this experiment did we introduce or manipulate any form of explicit reward as a result of completing a walk or run trial. Considering this, the proposed models assume that participants made decisions with the goal of exclusively minimizing costs. We present four possible models of utility, each making unique predictions for the slope of the walk/run indifference function. These candidate models are based on (1) minimizing COT, (2) minimizing cumulative total amount of metabolic energy, (3) minimizing cumulative total of movement time or (4) minimizing total time per distance (maximizing velocity). These four models each require some combination of the total distance travelled for each gait, average velocity for each gait (V_{w} for walk, V_{r} for run), and/or average metabolic rate for each gait ($\dot{E}_{\text{w}}$ for walk, $\dot{E}_{\text{r}}$ for run).

2.1.1. Minimizing cost of transport (J_{COT})

Calculating the indifference slope based on minimizing COT is dependent on minimizing the total metabolic energy normalized per unit distance. One way to calculate COT is to divide the metabolic rate by velocity:

$$J_{\text{COT}_x} = -\frac{\dot{E}_x}{V_x}. \tag{2.1}$$

Here, x denotes a placeholder for either walking (w) or running (r). A model of COT is exclusively determined by the velocity of the gait, which when at a constant velocity, is independent of changes in either total distance or total time. Self-selected walking velocities generally elicit lower COT than self-selected running velocities. Thus, this model would predict that an individual would always prefer to walk, regardless of the relative walking and running distances (figure 1*b*, green line parallel vertical axis). The negative sign in this model and subsequent models indicates that maximum movement utility is achieved by minimizing these costs.

2.1.2. Minimizing total energy (J_{energy})

Predicting indifference slopes by minimizing total energy is based on both the COT (equation (2.1)) and total distance covered using each gait. Measuring utility as a minimization of total energy can be achieved by calculating the COT of moving and multiplying that cost by the total distance moved:

$$J_{\text{energy}_x} = -\text{COT}_x\, D_x. \tag{2.2}$$

Predicting indifference according to minimizing total energy yields a linear function where walking distance is predicted by

$$D_w = \frac{\text{COT}_r}{\text{COT}_w} D_r. \tag{2.3}$$

When predicting walking distance as a function of running distance, a utility model that minimizes total energy will predict a slope above the line of unity, indicating that walking a longer distance at a lower COT will be equal to running a shorter distance at a greater COT (figure 1*b*, red line).

2.1.3. Minimizing total time (J_{time})

A utility model that is based on minimizing movement time requires two measurements to predict indifference, the velocity and distance of each walking and running bout:

$$J_{\text{time}_x} = -\frac{D_x}{V_x}. \tag{2.4}$$

Representing the minimization of movement time as a potential utility model to predict walking distance results in the function:

$$D_w = \frac{V_w}{V_r} D_r. \tag{2.5}$$

When predicting walking distance as a function of running distance, a utility model that minimizes total time will predict a slope for indifference below the line of unity indicating that walking a shorter distance at a slower velocity has equal utility as running a longer distance at a faster velocity (figure 1*b*, blue line).

2.1.4. Maximizing velocity (J_{vel})

Lastly, we consider a possibility where maximizing utility would always predict a preference to run. A utility based on this prediction can be described by minimizing total time per unit distance (maximizing velocity) and can be represented simply as

$$J_{\text{vel}_x} = V_x. \tag{2.6}$$

This utility would result in a horizontal line (figure 1*b*, gold line) and therefore would predict no change in equivalent walking distance as a function of increasing running distance.

2.2. Participants

Twenty participants (12M, 8F, 19–32 years, 73 ± 12 kg) gave written informed consent approved by the University of Colorado Institutional Review Board before participating in the experiment. All participants reported light-intensity exercise [21] at least once a week and no neurological, cardiovascular or biomechanical maladies. Experimentation took place in a lighted, climate-controlled, indoor track facility.

2.3. Task

Upon arrival, all participants first completed two laps around a 200 m track. The first lap was performed at a self-selected walking velocity and the second lap at a self-selected running velocity. When selecting their running velocity, participants were instructed to select a velocity that they felt they could comfortably maintain for over one mile (approx. 1.6 km). During each lap, participants were instructed to explore different velocities to find what they felt was most comfortable for each gait. Participants were instructed to use these walking and running velocities throughout the duration of the experiment.

The remainder of the experiment was designed to identify pairs of running and walking distances where running a given distance, D_r, was equally preferred to walking a given distance, D_w. These walk/run pairs of distances defined indifference points (figure 1*b*, asterisk). To measure a single indifference point, participants completed four sets of trial triplets. A triplet consisted of a single walking trial, a single running trial and a single choice trial (figure 2*a*). In walking trials, participants walked out to an indicated walk distance and back. In running trials, they ran out to an indicated run distance and back. In choice trials, they were given the freedom to repeat either the previous walk or run trial. The first trial in a triplet was randomly assigned as either the run or walk trial and the last trial in a triplet was always a choice trial. Each block consisted of four triplets of trials and each participant completed five blocks, with every block representing a single indifference point. Importantly, before the start of the first block, all participants were explicitly informed that the remainder of the experiment would last a total of 2 h and that their choice behaviours would not influence overall testing duration (i.e. choosing the shorter duration trial every time would not shorten the total time spent testing).

Figure 2*b* depicts the progression of one block of trials used to identify a single indifference point. The first triplet of trials in each block consisted of equal walk and run distances. Throughout a block, the run distance (figure 2, red markers) was fixed. Walk distances (figure 2, blue markers) were adjusted after each triplet of trials. The direction of the adjustment was contingent on the participant's choice trial (figure 2, grey regions). If the last choice was to run, the walk distance was *shortened* for the next triplet. If the last choice was walk, the walk distance was *lengthened*. The magnitude of the adjustment was greatest in response to the first choice and decreased with each subsequent choice. The adjustment after the first triplet was equal to the initial walk distance minus 20 m (minus 10 m in 40-m run block). The adjustment after the second triplet was one half the initial walk distance and the adjustment after the third triplet was one-quarter of the initial walk distance. No adjustment was made after the fourth (last) triplet.

We calculated a single indifference point upon completion of the fourth triplet in each block. The walk component of an indifference point was calculated at the end of each block by averaging the walk distances of the last walk choice and last run choice. The run component was equal to the tested running distance for that block. Five indifference points were calculated for each participant based on titrated walking distances equal to running distances of 40, 60, 80, 100 and 120 m. The order of run distances was randomized for each participant.

2.4. Model predictions

We measured the average walking and average running velocity at each block and used those values, along with the five tested running distances, to calculate walking distances that would result in an equal utility to running. A set of five walking distances were calculated according to each proposed utility model for every participant. We then fit a line through each of these sets of walking distances using a simple linear regression. This resulted in a slope for each utility model that could then be compared to the observed indifference slope of each participant. Note that the slope predicting walking distance based on minimizing COT would result in a vertical line and a slope based on maximizing velocity would result in a horizontal line.

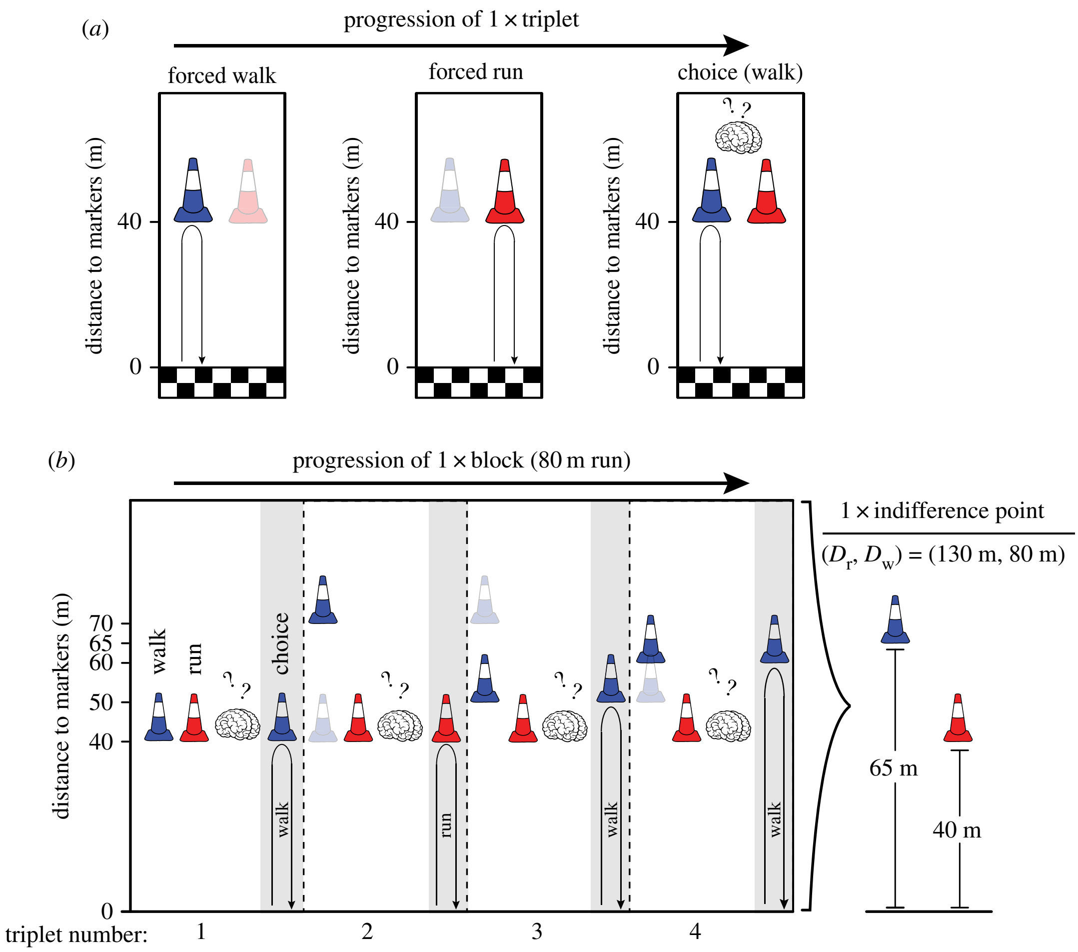

Figure 2. Protocol. (*a*) Progression of a single triplet of trials. This example triplet began with a walk trial, where the participant walked to the blue marker and back. The second trial was a run trial where the participant ran to the red marker and back. The third trial was a choice trial where the participant thought about which previous trial they preferred and then repeated that trial. The first trial within each triplet randomly began as either a walk or run trial. The last trial of each triplet was always a choice trial. The decision to either walk or run influenced the distance of the walk marker on the subsequent triplet. (*b*) Example progression of the 80-m block. Each block consisted of completing four triplets of walk/run/choice trials. After each triplet, the walk distance was adjusted based on the previous decision. Dashed lines indicate start of a new triplet. To calculate the walk component of a single indifference point (D_w), we averaged the walk distances between the last run choice and last walk choice. The run component of the indifference point (D_r) was based on the run distance, which was fixed within a block. Each new block used a different fixed run distance. Note that the distances on the vertical axis represent the distance to the marker. The actual distance covered was two times the distance to the marker, resulting from the participant moving out and then returning back to the start in a single trial.

To calculate the utility of each option, we did not directly measure metabolic COT, but instead estimated it according to equation (2.1). Metabolic rate ($\dot{E}_x$) normalized by mass was estimated as a function of velocity from previously published equations [6]. Metabolic rate in walking was estimated according to the function

$$\dot{E}_w = a_o + a_2 V_w^2, \tag{2.7}$$

where $a_o = 1.91\ \mathrm{W\ kg^{-1}}$ and $a_2 = 1.49\ \mathrm{W\ (m\ s^{-1})^{-2}}$. Metabolic rate for running was estimated according to the function

$$\dot{E}_r = b_o + b_1 V_r + b_2 V_r^2, \tag{2.8}$$

where $b_o = 5.17\ \mathrm{W\ kg^{-1}}$, $b_1 = 1.38\ \mathrm{W\ (m\ s^{-1})^{-1}}$ and $b_2 = 0.34\ \mathrm{W\ (m\ s^{-1})^{-2}}$.

2.5. Statistical analysis

We used a simple linear regression based on each participant's indifference points to predict the indifference slope that explains walking distance as a function of running distance when fit through the origin. We performed a Hartigans' dip test to measure whether the distribution of fitted indifference slopes was multimodal.

The best performing model for each individual was determined by comparing the 95% CI of the slope fit through a participant's indifference points against the slopes estimated for each of the four models. To test whether the fitted indifference slope indicated an individual's desire to minimize time, we measured the correlation between an individual's fitted indifference slope and preferred gait velocity using a simple linear regression. We also explored whether individuals adjusted their preferred gait velocity as a function of distance and whether this adjustment was based on how an individual represented each cost. Owing to the different walking distances experienced by each participant, this was achieved using a linear mixed effects model rather than a simple linear model with walking and running velocities predicted as a function of indifference slope and distance for each walking and running trial. All comparisons were conducted at a statistical level of $\alpha = 0.05$. Descriptive statistics are reported as mean ± s.e.

3. Results

Participants made decisions between walking and running different combinations of distances. We adjusted the relative distances of walking and running after each decision until individuals were indifferent between performing either gait. We refer to these final combinations of distances as indifference points and assume that at those combinations, the utility of walking is equal to the utility of running. We compared the fitted slope describing each participant's indifference points to slopes calculated from utility models that minimize COT, minimize total metabolic energy, minimize total movement time and maximize total velocity. Overall, our results suggest that the mechanisms responsible for how our group of individuals selected gait cannot be explained through the minimization of a single metabolic or temporal cost. Rather, participants minimized a weighted combination of these two conflicting costs, with the relative representation of each cost varying across participants.

3.1. Cost only models fail to predict decision-making strategies across group

Figure 3 illustrates how a single individual's gait decisions were used to calculate indifference points as a function of increasing running distance. The goal was to identify which utility model best represented the indifference slope where combinations of distances above the line would predict a running gait (figure 3, 'R' symbols) and combinations below the line would predict a walking gait (figure 3, 'W' symbols).

We described an individual's preference for each gait by fitting a line through the estimated indifference points (figure 3, black line). Fitted lines with relatively steeper slopes are more representative of minimizing total metabolic cost (figure 3, red line) and relatively shallower slopes are representative of minimizing total movement time (figure 3, blue line). Minimization of total COT cannot be described according to any slope because it predicts a preference to walk independent of any non-zero run distance (figure 3, green line parallel vertical axis). Maximization of velocity also cannot be described according to any slope because it always predicts a preference to run (figure 3, gold line parallel horizontal axis).

Across all participants, the average preferred walking velocity was 1.53 ± 0.03 m s^{-1} and the average running velocity was 3.32 ± 0.12 m s^{-1}. Using these velocities, we can predict walking distances as a function of running distance according to each proposed utility model. The average slope for the utility model minimizing total metabolic energy was equal to 1.16 ± 0.01 m of walking for each metre of running. When minimizing total time, we estimated a much smaller average slope of 0.46 ± 0.01 m of walking per each metre of running.

Every participant made at least one choice to run in each block, a choice that is counter to the minimization of COT. The walking component of each indifference point increased as a linear function of the running component in all participants except for P8 ($r^2 = 0.72 \pm 0.05$, range $= 0.29$–0.99). Indeed, not a single participant's fit exhibited confidence intervals that encompassed the COT indifference slope (figure 4, green vertical line). Six of the twenty participants had 95% CIs that encompassed minimization of total energy (figure 4, red line; P1, 2, 4, 5, 18, 20). Eight participants had 95% CIs that encompassed minimization of total time (figure 4, blue line; P9, 10, 11, 12, 13, 15, 16, 17). One participant had a slope that was best predicted by maximizing total velocity (figure 4, gold line; P8). The remaining five participants had indifference slopes that could not be explained by any of the proposed utility model (P3, 6, 7, 14, 19). No single participant had 95% CIs that encompassed more than one model. We can also apply a less-stringent criterion and assign a model to each participant based instead on

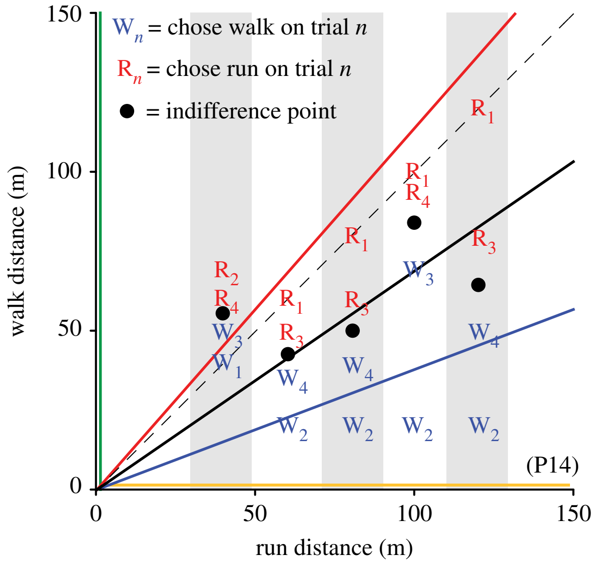

Figure 3. Depiction of how each block of triplets contribute to describing gait preference as a function of running and walking distance (representative participant, P14). The horizontal axis represents the run distance (m) of each decision and the vertical axis represents the accompanying walk distance (m). The preferred gait at each pair of distances is represented either as a 'W' if the participant preferred to walk or an 'R' if the participant preferred to run. The subscript accompanying each letter indicates at which triplet the choice occurred. The first decision of each block was always of equal walking and running distances (decisions along dashed unity line). The walk component of each indifference point (black markers) was calculated by averaging the walk distances of the last chosen run and last chosen walk trials. The run component was equal to the unchanged run distance within that block. Shaded vertical bars are intended to help contain the groups of decisions made within each block. The black line represents the slope of the regression line fit through all indifference points. Solid lines depict utility model predictions for this participant based on minimizing COT (green), minimizing total metabolic energy (red), minimizing total movement time (blue) and maximizing velocity (gold).

proximity of the indifference slope to the nearest utility model, calculated as the absolute difference between the participant's indifference slope and each utility model's slope. In this case, we find that eight participants are best explained by total energy, eleven are best explained by total movement time and one is best explained by maximizing velocity.

While it appears that no single cost was able to explain decision-making across our entire group of participants, it is possible that clusters of participants may have selected a single cost (energy or time). If this was the case, we would expect there to be a clear bimodal distribution in slopes between the participants that minimized energy and the participants that minimized time. We found that the slopes across our participants (not including P8) ranged from 0.3 to 1.8. When testing across this range of slopes, we found the distribution to be unimodal (Hartigans' dip test, $p = 0.44$). Based on this result, we cannot conclude that there were two discrete time and energy strategies. Instead, there was a range of relative weightings between these costs.

3.2. Including time for waiting does not improve performance of total energy model

The duration of the entire experiment was constrained to 2 h and was unaffected by an individual's preferences between gaits. One consequence of preferring the gait with the shorter

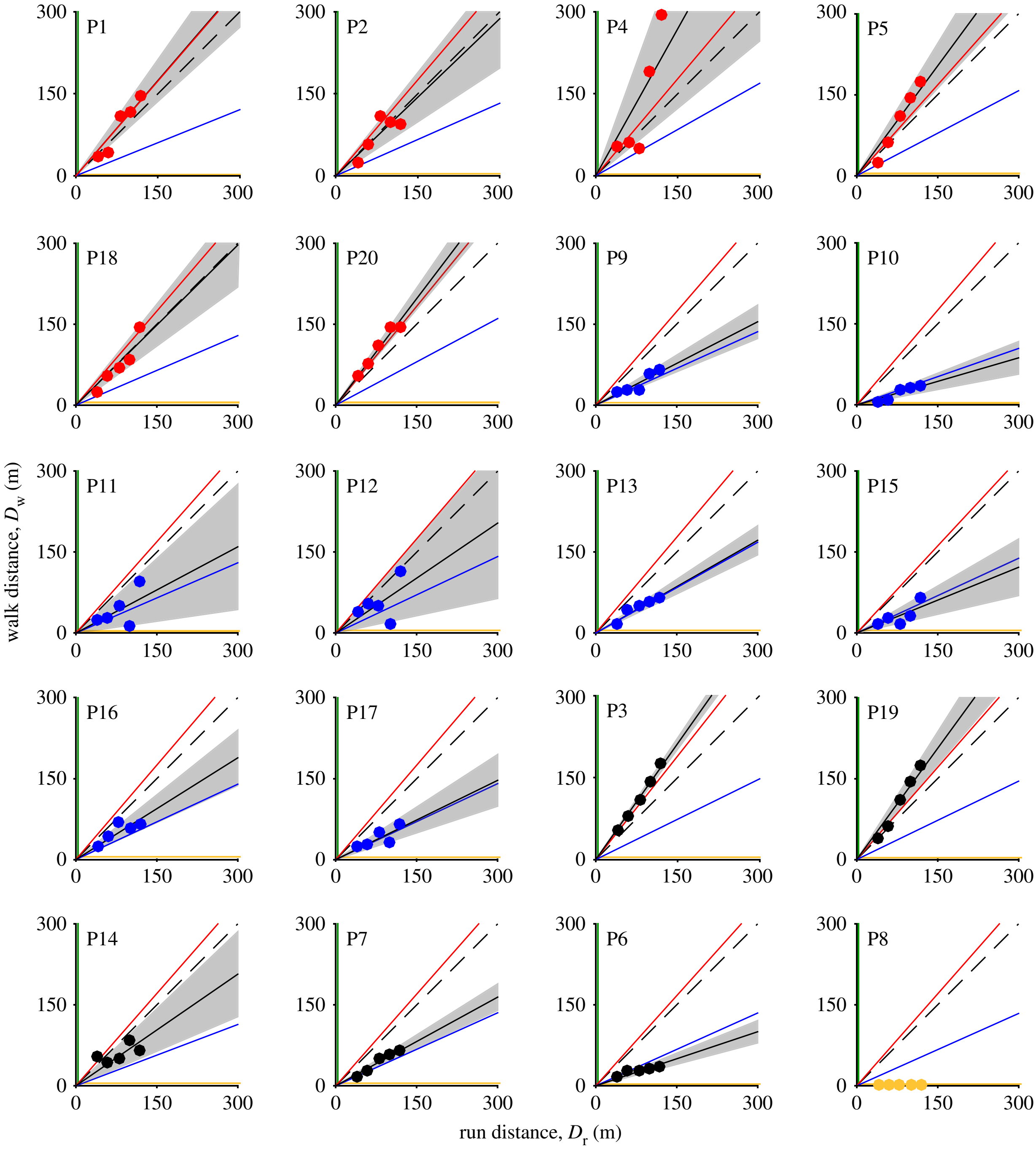

Figure 4. Model predictions for walk and run combinations of equal utility. Green lines represent indifference slope predictions based on minimizing COT, red lines represent predictions for minimizing total metabolic energy, blue lines represent predictions for minimizing total time and gold lines represent predictions for maximizing velocity. Black lines and shaded grey areas represent best fit and 95% CIs for the indifference slope according to the estimated indifference points. Six participants had CIs that fell within the total energy model (indicated by red indifference points), eight participants had CIs that fell within the time model (blue indifference points) and five participants had CIs that did not fall within any of the cost minimization models (black indifference points). Participant eight (P8) always chose to run, independent of any manipulations to walk distances (maximized velocity, indicated by gold indifference points). Axes are equally scaled across all participants.

duration was that there was a subsequently longer waiting time before the next trial. To consider the metabolic consequences of waiting, we calculated the difference in movement time between the shorter and longer movement, multiplied that difference by a typical metabolic rate for standing at rest ($\dot{E}_{\text{wait}} = 1.22\ \text{W kg}^{-1}$ [6]), and added that cost to the total energy of the movement with the shorter duration. Considering the added metabolic cost of waiting, the average total energy slope increased to 1.24 ± 0.13 m of walking per metre of running. This new total energy model still only falls within the 95% CI of the indifference slope for four participants (P1, 5, 19, 20), indicating that minimizing total energy alone does not appear to represent the utility model used for gait decisions across our participants.

3.3. Individuals who minimized movement time did not walk faster, but they did run faster

Minimization of total energy predicts a relatively steep indifference slope, indicating that moving slower (walking) for longer distances is equal to moving faster (running) for shorter distances. Minimizing total movement time makes

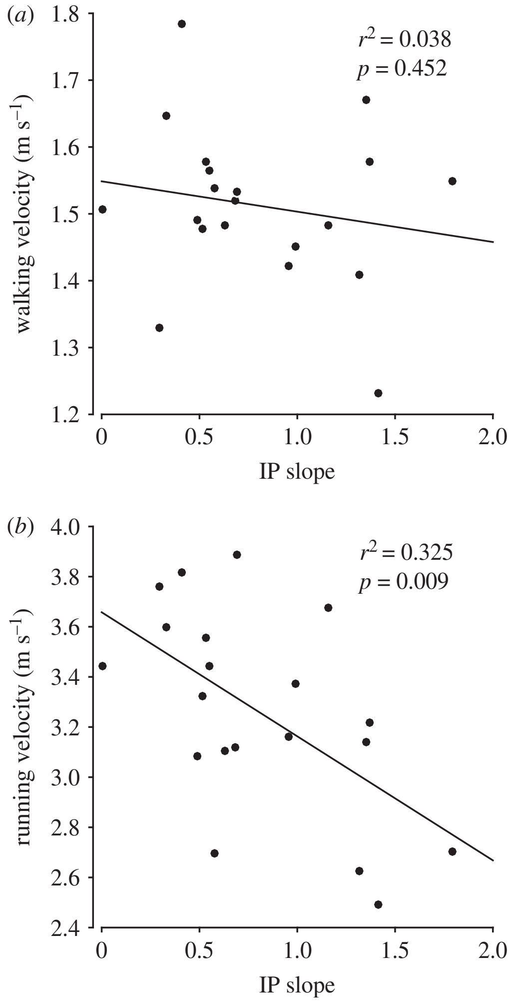

Figure 5. Correlations between indifference point (IP) slope and average preferred gait velocity (m s^{-1}) in (*a*) walking and (*b*) running. Each marker indicates a single participant.

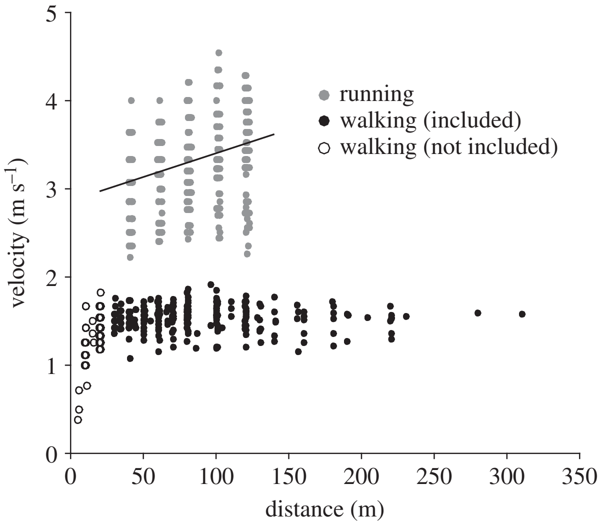

Figure 6. Relationship between preferred gait velocities (m s^{-1}) and total distance (m). Walking velocity was modelled as a function of distance using data points that were measured at or above a distance of 30 m (filled circles). Walk trials below 30 m were not included in the fit (open circles). Across fitted trials, walking velocity was on average 1.57 $\pm$ 0.03 m s^{-1} and did not change as a result of increasing distance. Running velocity was also modelled as a function of distance and included all 380 running trials (grey-filled circles). The black line is the model prediction for the median fitted indifference slope indicating that running velocity generally increased when trials required moving further distances. Graphically, all running and walking points were given a small amount of artificial noise along the horizontal axis to indicate regions where multiple trials were completed at identical velocities.

an opposite prediction, indicating that moving slower for shorter distances is equal to moving faster for longer distances. An individual who considers time in their decisions will have a shallower slope to describe their indifference points. Assuming gait velocity reflects the desire to minimize movement time, we tested whether there was a correlation between each participant's indifference slope and their self-selected gait velocity. We found no correlation between an individual's indifference slope and their average preferred walking velocity (figure 5*a*, $r^2 = 0.038$, $p = 0.452$), but we did find a moderate negative correlation between an individual's indifference slope and their average preferred running velocity (figure 5*b*, $r^2 = 0.325$, $p = 0.009$).

3.4. The distance of a running trial influenced preferred running velocity

The range of walking distances was established according to individual gait preferences during choice trials. Across all participants, distances for a single walking trial ranged from 5 to 310 m. The length of each running trial was the same for all participants and ranged from 40 to 120 m. We would predict that individuals only sensitive to minimizing total metabolic energy (steeper slopes) would adapt a preferred gait velocity independent of total distance. For individuals willing to discount metabolic energy to decrease total movement time, we would expect preferred velocities to increase (become more metabolically costly) at greater distances to offset the added temporal costs of longer movements.

We performed a linear mixed effects regression to explain average gait velocities using distance and indifference slope as predictors. To minimize the influence of acceleration on average velocity, we excluded trials that were shorter than 30 m (15 m out and 15 m back). This resulted in the removal of 88/380 trials across all participants, all of which were walking trials. With the remaining trials, we observed that walking speed was unaffected by either walking distance, indifference slope, or an interaction of the two predictors ($ß_o = 1.601$ m s^{-1}, $p < 0.001$; $ß_{distance} = 0.001$ s^{-1}, $p = 0.052$, $ß_{IP} = -0.114$, $p = 0.123$, $ß_{interaction} = -0.007$, $p = 0.160$). Contrary to the absent effects of distance on preferred walking velocity, we found a positive relationship between preferred running velocity and running distance ($ß_o = 3.037$ m s^{-1}, $p < 0.001$; $ß_{distance} = 0.008$ s^{-1}, $p < 0.001$, $ß_{IP} = -0.264$, $p = 0.158$) meaning that preferred velocity increased when running over longer distances (figure 6); however, the extent of this increase depended on the indifference slope of the individual ($ß_{interaction} = -0.004$, $p < 0.001$). Specifically, individuals who placed a higher value on time (shallow slopes) chose a faster running velocity in response to longer distance tasks compared to individuals who placed a lesser value on time (steep slopes).

3.5. Preferred gait velocity and decision-making tendencies were unaffected by the 2-h duration of the experiment

Within the 2-h duration of the current experiment, participants completed 60 combined trials of walking and running. This amount of locomotion introduces the possibility that individuals may have become fatigued, changing how movement costs were relatively weighted throughout the course of the experiment. To detect potential effects of fatigue, we measured changes in velocity for each gait as a function of block and observed that changes in both walking and running velocities were on average consistent throughout the entire experiment (figure 7, rmANOVA, main effect of block, walking, $F_{4,72} = 0.789$, $p = 0.536$; running, $F_{4,72} = 0.01$, $p = 0.99$). This result suggests that if preferred velocity reflects how an individual weighs movement costs, the weighting of these costs was consistent throughout the experiment.

We also tested whether the frequency of choosing either gait changed across blocks. Independent of relative walk and run distances, the probability that a participant chose to walk was 45.53 ± 0.51% and this frequency was consistent throughout the duration of the experiment (rmANOVA, main effect of block, $F_{1,360} = 0.420$, $p = 0.518$). These results further provide evidence that the duration of the experiment did not affect how an individual considered metabolic energy and movement time when selecting between gaits.

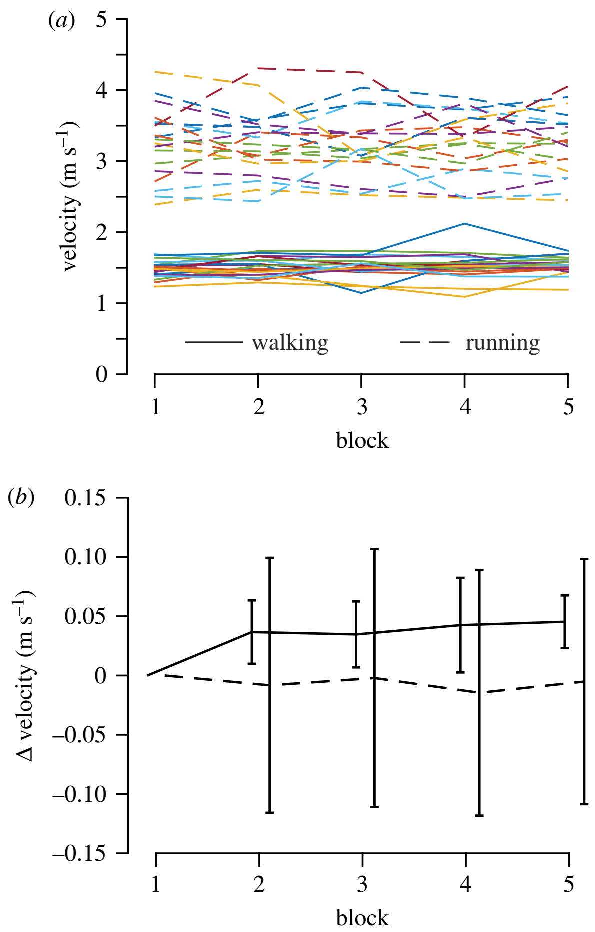

Figure 7. Effect of block on preferred walking velocity (solid lines) and running velocity (dashed lines). (*a*) Coloured lines represent walking and running velocities for individual participants. Across the group, there was a much larger spread of preferred running velocities when compared to the spread of walking velocities. (*b*) The average change in walking and running velocities across blocks represented as difference from the average velocity of the first block.

4. Discussion

The primary goal of the present study was to explore how humans weighed changing metabolic and temporal costs when deciding between walking and running gaits. Our protocol consisted of individuals making gait decisions across numerous combinations of walking and running distances. Their gait preferences allowed us to estimate indifference points, defined as walk and run distance combinations where the preference for performing a walking gait was equal to the preference for performing a running gait. We quantified the metabolic and temporal consequences of each gait at each distance to explore whether minimizing either cost explained gait preference. For each individual, walking distance was accurately described as a linear function of running distance; however, the slope of this function varied widely between participants. When modelling each individual's set of indifference points, roughly a third of our participants had indifference slopes that corresponded with minimizing total energy, another third appeared to minimize total movement time and the remaining third could not be explained by minimization of either cost. The diversity of gait preferences across the group means that decision-making strategies were likely not a result of minimizing a single movement cost, but rather a participant-specific weighting of the two.

We used the slope of the regression line fit through each participant's observed indifference points to explain how each cost contributes to the total movement utility of each gait. A relatively steep slope indicated a strong weighting on metabolic energy with little cost for time. A relatively shallow slope indicated the opposite, a strong weighting on time with less cost for metabolic energy. We found an average slope across participants of 0.83, falling below the slope predicted by the minimization of metabolic energy (1.16) and above the slope predicted by the minimization of time (0.46).

Several participants ($n = 8$) had indifference slopes that indicated their decisions were influenced by movement time, despite being informed that their decisions would not impact the total duration of the experiment. One explanation for this behaviour is that completing each trial had an arbitrary utility that decreased over time, a phenomenon classically referred to as temporal discounting [22,23]. Recent results have demonstrated a role for temporal discounting in the selection of reaching velocity [18,24], building upon a growing body of research in movement decision-making [25–27]. The magnitude of temporal discounting has been reported to vary substantially between humans, with this variability accurately predicting how quickly an individual will generate movements towards a reward [20]. If temporal discounting influenced how our participants decided between gaits, we would expect their sensitivity to temporal costs to manifest in how they selected velocity for each gait. We found that the running velocity of each participant was moderately explained by their indifference slope. Specifically, individuals who had a greater tendency to minimize time (shallower slopes) also selected faster running velocities. We did not find any correlations between indifference slope and walking velocity.

For movements of a set distance, individuals may have chosen to move faster to minimize the loss in utility due to temporal discounting. However, increasing velocity also influences the total metabolic energy required for the movement and implies that increasing velocity above what is metabolically optimal only improves total utility if the benefits of arriving earlier are greater than the penalty of moving at a higher metabolic COT. The COT curve as a function of velocity is relatively steep in walking when compared to running (figure 1*a*). These differences predict that decreasing movement time in walking would come with a greater increase in metabolic energy compared with a similar change in movement time when running. This may explain why we found that indifference slope predicted running velocity, but not walking velocity.

Temporal discounting can also explain variability in running velocities observed within each participant. Participants adjusted their preferred running velocity as a result of increasing distance, but not their preferred walking velocity. If we assume that individuals were exclusively minimizing metabolic energy, they would move at a velocity corresponding to the minimum COT independent of total distance. However, as previously highlighted, temporal discounting will lead to greater losses in utility for longer duration movements. Decreasing total movement time over a shorter distance requires a greater change in gait velocity when compared with the same decrease in time over a longer distance. However, this explanation fails to account for the shape of the temporal discounting function, which commonly predicts that a discrete change in duration has greater effects when applied at earlier time-points when compared with those same changes at later time-points [22].

Another explanation for why individuals discount the metabolic cost of running may be because the activity of running itself carries an implicit reward through improving mood or affect [28,29]. When a group of regular runners were prevented from exercising for a two-week period, they reported symptoms similar to what is observed in individuals who are suffering from the withdrawal of addictive drugs [30]. The neurological basis of this exercise induced reward may be explained through the release of endocannabinoids, neurotransmitters that are known to influence the release of dopamine in the reward pathways of the brain [31,32]. Within an individual, the level of endocannabinoids released increases with exercise intensity; however, when comparing across individuals, these responses appear independent of fitness level [33].

Our protocol involved all participants running between 40 and 120 m per trial. In walking, depending on the decisions of each participant, distances ranged between 5 and 310 m per trial. Orendurff *et al*. [34] reported that in healthy adults, over 90% of recorded movement bouts throughout the day involved taking fewer than 100 consecutive steps. Del Din *et al*. [35] similarly reported that only 3% of movement bouts in healthy older adults had a duration of greater than 60 s. While our tested distances are within the range of what would be considered a representative movement bout, the actual limits of what a healthy adult human can cover are obviously much greater. Obtaining indifference points over a larger range of walking and running distances would allow us to better understand whether utility increases linearly as a function of distance (as presently assumed) or, instead, interacts with the weighting between metabolic and temporal costs.

In each trial, participants had to ambulate to the indicated marker, turn around, and return. This exchange required four different moments of significant acceleration; an initial acceleration to preferred velocity, deceleration when approaching the marker, re-acceleration when leaving the marker and a final deceleration at the end of the trial. In longer movements, these accelerations likely had minimal impact on average velocity. However, when the movements were short, calculating average velocity as the total distance over total time may not accurately represent the constant velocity exhibited in the absence of acceleration. The equation we chose for calculating metabolic rate was collected while individuals walked and ran at constant velocities. Using these equations for movements with accelerations underestimates metabolic rate [36]. By not considering how accelerations influence the total metabolic cost of a movement, our model predictions may slightly underestimate the actual metabolic cost of moving, especially when over shorter distances.

We estimated the metabolic cost of walking and running using previously published functions [6]. By estimating rather than directly measuring metabolic rate, we may have failed to capture differences due to the stature [37,38] and/or body mass index [3,39] of our participants. However, if we assume that any error in metabolic cost is equal in the direction between gaits (overestimation for both gaits or underestimation for both gaits), deviations in our estimations would likely have minimal consequences on the slope of how total metabolic energy predicts indifference.

If an individual did not have extensive experience with running, than it is possible that their ability to accurately represent the consequences of running is different when compared to an individual that regularly runs. We required participants to experience both walk and run options before making a decision with the intention that they would use this recent experience, rather than their past experiences prior to the experiment, when considering between each gait.

One final consideration is that participants always started and ended each trial at the same position. Because a common purpose of walking and running is to change the location of the animal, it is possible that our current protocol is not capturing an additional contributor towards the utility of a movement, net displacement. By having all trials result in a net displacement, we may see a change in how the relative influence of time and energy contribute to gait selection. A potential follow-up where trials do not start and end at the same position might help elucidate how net distance influences utility in gait selection.

5. Conclusion

Our results provide evidence that when deciding between walking and running, humans make decisions according to a utility model that is more complex than solely minimizing metabolic energy or time. In response to different relative walking and running distances, participants made decisions that can be described according to a weighted combination of the metabolic and temporal costs tied to each gait, with an individual's tendency to minimize time influencing both how they established preferences between movements and subsequently, how those movements were executed.

Ethics. All participants gave written informed consent approved by the University of Colorado Institutional Review Board before participating in the experiment.

Data accessibility. All data and analysis code used in this manuscript can be found at https://drive.google.com/open?id=1bFr_Lcq44gMLYuO-T0REgFQxWtj9sV_S4.

Authors' contributions. E.M.S., R.K. and A.A.A. designed protocol and prepared figures and wrote manuscript. E.M.S. collected data and analysed data.

Competing interests. We declare we have no competing interests.

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