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RESEARCH ARTICLE

Preferred walking speed on rough terrain: is it all about energetics?

Koren Gast[1], Rodger Kram[2] and Raziel Riemer[1,*]

ABSTRACT

Humans have evolved the ability to walk very efficiently. Further, humans prefer to walk at speeds that approximately minimize their metabolic energy expenditure per unit distance (i.e. gross cost of transport, COT). This has been found in a variety of population groups and other species. However, these studies were mostly performed on smooth, level ground or on treadmills. We hypothesized that the objective function for walking is more complex than only minimizing the COT. To test this idea, we compared the preferred speeds and the relationships between COT and speed for people walking on both a smooth, level floor and a rough, natural terrain trail. Rough terrain presumably introduces other factors, such as stability, to the objective function. Ten healthy men walked on both a straight, flat, smooth floor and an outdoor trail strewn with rocks and boulders. In both locations, subjects performed five to seven trials at different speeds relative to their preferred speed. The COT–speed relationships were similarly U-shaped for both surfaces, but the COT values on rough terrain were approximately 115% greater. On the smooth surface, the preferred speed (1.24±0.17 m s^{-1}) was not found to be statistically different (*P*=0.09) than the speed that minimized COT (1.34±0.03 m s^{-1}). On rough terrain, the preferred speed (1.07±0.05 m s^{-1}) was significantly slower than the COT minimum speed (1.13±0.07 m s^{-1}; *P*=0.02). Because near the optimum speed the COT function is very shallow, these changes in speed result in a small change in COT (0.5%). It appears that the objective function for speed preference when walking on rough terrain includes COT and additional factors such as stability.

KEY WORDS: Cost of transport, Stability, Optimization, Balance, Locomotion

INTRODUCTION

Humans have evolved the ability to walk very efficiently. Over generations, our bodies have evolved muscular and skeletal systems well suited to locomotion (Alexander, 2003). Further, we learn and choose to walk in a way that minimizes our metabolic energy expenditure (Ralston, 1958; Zarrugh et al., 1974). For example, it has been shown that step frequency (Zarrugh et al., 1974), step length (Umberger and Martin, 2007), step width (Donelan et al., 2001) and speed (Zarrugh et al., 1974) are all chosen to minimize energy expenditure.

More specifically, it has been found that humans choose a walking speed (i.e. preferred speed) that is close to the metabolically optimal speed that minimizes the gross cost of transport (COT) – the metabolic rate divided by the locomotion speed. This phenomenon has been observed in people of normal weight, in people who are obese (Browning et al., 2006), in people with trans-tibial and trans-femoral amputations (Genin et al., 2005), in people with post-polio syndrome (Ghosh et al., 1982), and when people carry loads (Bastien et al., 2005). These studies all support the idea that while walking, our body optimizes $\mathrm{MIN}_{\{\theta\}}[\mathrm{COT}(\theta)]$, where θ is a vector of walking parameters.

However, there are exceptions to this rule. For example, Clark-Carter et al. (1986) found that people who are blind prefer walking speeds similar to sighted people when they are accompanied by a guide. However, without a guide, their preferred walking speed is slower and is unlikely to correspond to their COT minimum. More recently, it has been discovered that when walking downhill, humans do not select a gait pattern that minimizes COT. Monsch et al. (2012) found that when instructed to walk downhill with a 'loose relaxed gait', subjects had a lower COT than when walking with their natural, preferred gait without any instructions. Similarly, it was found that people walk more slowly on a smooth surface when it is elevated above the ground (Brown et al., 2002; Schniepp et al., 2014) and thus presumably they chose not to walk at the energetic COT minimum. Kalantarov et al. (2018) found that pedestrians crossing a street increased their walking speed when the time gap between cars was smaller.

These studies led us to propose that humans choose walking parameters to optimize an objective function that is more complex than $\mathrm{MIN}_{\{\theta\}}[\mathrm{COT}(\theta)]$. Such an objective function could, for example, take the following form:

$$\mathrm{MIN}_{\{s\}}[w_1 \times \mathrm{COT}(s) + w_2 \times 1/\mathrm{Stability}(s) + w_3 \times \mathrm{Time}(s)], \quad (1)$$

where s is the walking speed, and w_1, w_2 and w_3 are weighting coefficients that represent the importance of the different factors for a given task. This formulation proposes that when choosing walking parameters, we optimize not only for COT but also for stability and time of completion. Note that we do not claim this is the function that humans are trying to optimize; rather, it is one possible alternative to a function that only minimizes COT. This idea is in agreement with Shadmehr et al. (2016), who proposed an objective function for humans performing a reaching motion that is different from COT minimization alone.

To date, most research into walking and the COT phenomenon has been carried out on treadmills or smooth, level floors. There are several studies that investigated the metabolic rate of locomotion on natural terrains, but they did not focus on the relationship between optimal speed and preferred speed. For example, walking has been investigated on sand (Pinnington and Dawson, 2001), grass (Davies and Mackinnon, 2006), dirt roads (Daniels et al., 1953) and snow (Pandolf et al., 1976; Soule and Goldman, 1972). Givoni and Goldman (1971) and Pandolf et al. (1977) developed prediction

[1]Department of Industrial Engineering and Management, Ben-Gurion University of the Negev, P.O.B. 653, Be'er-Sheva 8410501, Israel. [2]Department of Integrative Physiology, University of Colorado Boulder, Boulder, CO 80309-0354, USA.

*Author for correspondence (rriemer@bgu.ac.il)

R.R., 0000-0002-9358-6287

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List of symbols and abbreviations

COT	cost of transport
COT_{norm}	normalized cost of transport
E_m	energy expenditure per unit distance
G	gradient
k	number of variables
L	external load
LMM	linear mixed model
M	body mass
mc	meaningful coefficient
MR	metabolic rate
RER	respiratory exchange ratio
RMSE	root mean square error
s	speed
s_{norm}	normalized speed
SSE	sum of squared errors
η	terrain factor

equations for the metabolic cost of load-carrying while walking on different terrains and slopes. A recent study examined the metabolic cost of walking on a treadmill that imitates uneven terrain (Voloshina and Ferris, 2013). However, to the best of our knowledge, no one has examined COT as a function of speed on natural, rough terrain.

In this study, we compared the COT for walking at different speeds on a smooth level floor versus natural, rough terrain. Investigation of COT on natural surfaces is important for two main reasons. First, human walking efficiency primarily evolved on natural surfaces, not smooth floors or treadmills. Second, walking on rough terrain intrinsically requires the person to consider their stability while walking. Although there is no explicit model for stability as a function of speed on rough terrain, we know from experience that humans tend to walk slower when there is a greater consequence of falling (Brown et al., 2002; Schniepp et al., 2014). Thus, we hypothesized that on rough terrain, the preferred walking speed would be slower than on smooth terrain and slower than the metabolic COT minimum speed. If this is found to be the case, it would imply that the objective function for human walking does include some sort of ‘stability’ factor, which is greater on rough terrain than on smooth, level surfaces.

MATERIALS AND METHODS

Subjects

Ten healthy male subjects (body mass: 75.10±11.64 kg, height: 1.82±0.07 m, age: 27.5±1.6 years; mean±1 s.d.) participated in this experiment. All test subjects were instructed to sleep for at least 6 h on the night prior to the experiment and to eat a light breakfast ending at least 2 h prior to the start. The Ben-Gurion University Human Subjects Research Committee approved the study and participants gave written informed consent. Each subject performed three walking sessions: one session on a smooth, level floor and two sessions on rough terrain.

Protocol

For the smooth, level concrete floor condition, the route was 44.0 m long, straight, flat and in the shade. For the rough terrain condition, the subjects walked out and back along a 67.0 m long trail, measured with a tape measure along the path itself. The straight-line horizontal distance from start to turnaround was 60.3 m. The actual walking path was relatively straight but had some small elevation and left–right deviations. We measured the changes in elevation along the trail and found that the maximum elevation amplitude was less than 2 m (Fig. 1A). The trail comprised some naturally scattered rocks and boulders (Fig. 1B; for a short video of a subject walking, see Movie 1).

Experimental procedure

Subjects did not need any practice to walk comfortably on the smooth floor. However, the rough terrain condition required practice. Although all of the subjects had prior experience of rough terrain walking, they did not partake in this activity daily. In a pilot study, we found that there was a learning effect and that it took approximately 25 min of practice before the COT stabilized. Therefore, to eliminate the possibility of acquiring data during this learning period, subjects completed two rough terrain sessions during which they performed the full experimental protocol. For our analysis, we used only the second session data. At the beginning of each the two sessions, after the subject had been fitted with the metabolic measurement system, they walked out and back along the trail with a guide (one of the research team members) who showed them the route, which was marked with small flags. The subjects then walked the trail by themselves for at least 10 min at various speeds. They started with their preferred speed, completing the full out-and-back circuit twice. This was followed by their maximum walking speed and then finally a very slow speed (approximately 50% of their preferred speed). At the maximum and very slow speeds, each subject completed one full out-and-back circuit. In a pilot study, we found that this protocol accelerated learning and reduced adaptation time. The protocol was inspired by Selinger et al. (2015), who studied humans walking with novel exoskeletons and found that in order to find the optimal step frequency, which minimized their metabolic rate, subjects had to carry out an exploratory session in which they walked at fast and slow step frequencies.

After the practice trial, the main experiment started. The subjects performed six additional trials on the smooth, level ground and seven on the rough terrain; each took 7–9 min. For each of these surfaces, the first and last trials were always at the preferred speed. We calculated the average speed (e.g. preferred speed) from the time for completion of the trail’s known distance. We also tested four other speed categories: maximum, which was the subject’s maximal walking speed (approximately 140–190% of preferred speed); fast, which was a speed between maximum and preferred speed (approximately 120–150% of preferred speed); slow (approximately 75% of preferred speed); and very slow (approximately 50% of preferred speed). For the rough terrain, to determine the repeatability of preferred speed and metabolic measurements, subjects performed an additional preferred speed trial in the middle. There was a 5-min rest period between trials. For further information about the trial speeds and order, see Appendix 1.

Walking speed was controlled by dividing the trail into two sections, so for an out-and-back lap of the trail, we set four target times (‘quarters’) based on the designated walking speed. The subject’s speed was coached via verbal commands from the researcher based on these target times. If the subject walked a section more slowly than required, they were encouraged to quicken their pace to meet the goal at the next check point. After approximately four to five quarters, the subject’s speed remained relatively steady and no further coaching was needed. After the speed had stabilized, the average standard deviation of all quarters for each trial was 5% or less. Seethapathi and Srinivasan (2015) found that fluctuations in walking speed can lead to increase of 5–20% of the metabolic rate. However, the speed fluctuations in their experiments were approximately 15–45% relative to the average speed. These changes in speed occurred with a cycle time of 4–8 s. In our case, the fluctuations in walking speed were significantly smaller and probably had a negligible effect on metabolic expenditure. We found that steady-state rates of energy expenditure were obtained after approximately 1.5–2 min.

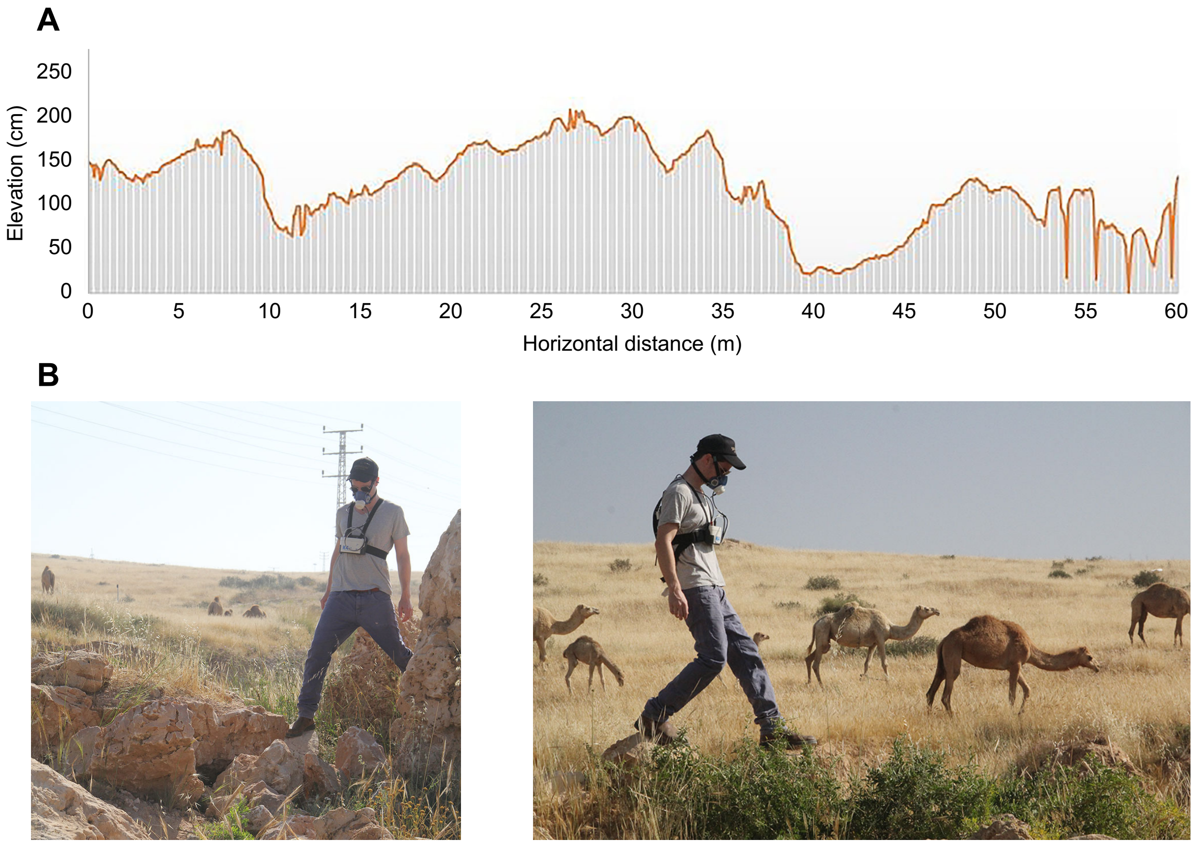

Fig. 1. The rough terrain trail. (A) Elevation profile surveyed at 10 cm horizontal distance intervals along the trail. Elevations are relative to the lowest point baseline. Subjects stepped over deep, narrow cracks or small, sharp rocks. (B) One of the subjects walking on the trail. The size of the rocks and boulders ranged from 2 to ∼50 cm. Sometimes the subject stepped on the boulders and sometimes in between them (see Movie 1).

Therefore, we only analyzed measurements of metabolic rate that were obtained at least 3 min after the start time. To eliminate the effects of local terrain variation, we averaged metabolic rate values over full out-and-back laps. Thus, the subject always walked a distance that was a multiple of 134 m (e.g. 134, 268, 402 m etc.). The same procedures were employed for the smooth floor condition (e.g. multiples of 88 m: 88, 176, 264 m etc.).

We measured the metabolic energy consumption using a K4b2 telemetric indirect calorimetry system (Cosmed, Rome, Italy). This system is portable and consists of a processing unit containing the O_2 and CO_2 analyzer and a battery pack. Together, the unit has a mass of 1.5 kg and was worn by the subject along with a silicone mask containing a flow-rate turbine. Every day and before each trial, the turbine was calibrated using a standard authorized calibration gas mixture and a volume pump.

Data analysis

Metabolic rate was calculated using the Brockway (1987) equation. We then calculated the COT by dividing the average metabolic rate (MR) by the average speed and the subject's body mass, i.e.:

$$\mathrm{COT}(s) = \frac{\mathrm{MR}(s)}{s \cdot M}, \tag{2}$$

where s is the walking speed and M is body mass. The reported metabolic values ($\mathrm{J\,m^{-1}\,kg^{-1}}$) are all gross metabolic rates; no resting/standing rates were subtracted. Preferred speed and metabolic rates were calculated as the average of the replicated trials (two for smooth floor and three for rough terrain). To ensure that the metabolic energy was primarily generated via aerobic metabolism, only trials with a respiratory exchange ratio (RER) of less than 1.00 were analyzed.

Several methods were used to develop the metabolic prediction equation; however, they were all fit to predict the metabolic rate of the average subject (Schertzer and Riemer, 2014; Ralston, 1958; Pandolf et al., 1977). Thus, to describe the metabolic rate data using the best fit model in our study, we tested linear mixed models (LMMs) with polynomials of orders 1 to 4 for each surface's dataset. We used LMMs because they are useful when repeated measurements are made on the same statistical units. LMMs allow both fixed and random effects, which means that they take into account that the same subject had been measured several times for different walking speeds. Moreover, LMMs enable the development of a personal model for each subject that also considers the group data and not only the specific subject data (West et al., 2014). Using LMMs, we tested which polynomial order gave the best fit to the data, i.e. the lowest Bayesian information criterion (BIC) value (Burnham and Anderson, 2004). We developed prediction equations for metabolic rate and COT for the group and for each subject.

To test whether there was a significant difference between the regression equations for the relationship between metabolic rate and speed between the two surfaces, we applied a Chow test.

The Chow test F-statistic was calculated as:

$$F = \frac{(\mathrm{SSE_a} - (\mathrm{SSE_{rt}} + \mathrm{SSE_f}))/k}{(\mathrm{SSE_{rt}} + \mathrm{SSE_f})/(N_1 + N_2 - 2 \times k)}, \tag{3}$$

where $\mathrm{SSE_a}$ is the sum of squared errors (SSE) calculated on all the observations, $\mathrm{SSE_{rt}}$ is the SSE of the observations from the rough terrain experiments, SSE_f is the SSE of the observations from the experiments on the smooth floor surface, k=4 is the number of variables in the regression equations, and N_1=66 (rough terrain), N_2=58 (smooth floor) are the number of observations in each group. Further, to test whether the differences between the fits of the two surfaces are meaningful, we compared the difference between the predictions of the two models with the error in their predictions of the experimental results, using the following equation:

$$\mathrm{mc} = \frac{\left(\sum_1^n (y_{1i} - y_{2i})^2\right)/n}{(\mathrm{MSE}_1 + \mathrm{MSE}_2)/2}, \quad (4)$$

where mc is the meaningful coefficient and a low number (e.g. 1) means that the difference between the models is the same as the average error in each of the model predictions, y_1 and y_2 are the models for each of the surfaces, i is the index for the speeds [$y_1(s_i)$=y_{1i}], n is the total number of elements in the speed vector, and MSE_1 and MSE_2 are the mean square error of the models (error between the model and the experimental data).

To test whether there was a significant difference between the preferred and energetically optimal speeds for each surface, we compared the preferred speeds with the optimal speeds of each individual. We hypothesized that on rough terrain, the preferred walking speed would be slower than the metabolic COT minimum speed. Thus, for the comparison, we used a paired two-tailed t-test. Optimal speed was defined as the speed corresponding to the minimum COT value calculated using the fitted LMM for each individual and each surface (i.e. the speed where the function's first derivative equals zero).

Finally, we used another Chow test to determine whether the COT versus speed relationships were different on the two surfaces, because the preferred speeds and metabolic rates were different. To perform this comparison, all values were normalized as follows: for each subject, all walking speeds were divided by the subject's preferred speed and all COT values were divided by the COT of the subject at his preferred walking speed. We also calculated the meaningful coefficient (Eqn 4).

RESULTS

Metabolic rate

For a linear increase in walking speed, we observed a polynomial increase in metabolic rate (Fig. 2). After testing LMMs with four different polynomials orders, we found that for walking on both the smooth floor and rough terrain, the best fit to the data (i.e. lowest BIC; Appendix 2, Table A1) was of the form: $\mathrm{MR}(s)$=bs^2+cs+d, where metabolic rate is normalized to mass (W kg^{-1}) and s is the walking speed (m s^{-1}). Here, we present the metabolic rate functions for the group:

$$\mathrm{MR}_{\mathrm{floor}} = 2.45s^2 - 3.02s + 3.52, \quad (5)$$

$$\mathrm{MR}_{\mathrm{rough\ terrain}} = 4.55s^2 - 3.20s + 5.06. \quad (6)$$

The Chow test showed that there was a significant difference between the smooth and rough terrain conditions (P<10^{-15}); therefore, it was reasonable to fit a different set of function constants for each surface. Further, the meaningful coefficient (Eqn 4) was 44.07, which means that the average difference between the models was approximately 44 times larger than the average error in the predictions of each model.

We collected a total of 130 trials: 70 on rough terrain and 60 on smooth floor. We could not use the results of six trials. We excluded three trials owing to RER values >1: one because of a subject fall and two because of data recording failure. Thus, we fully analyzed 66 trials on rough terrain and 58 trials on smooth.

COT

For both surfaces, the best fit to the data (i.e. lowest BIC; Appendix 2, Table A2) was of the form $\mathrm{COT}(s)$=bs^2+cs+d, where COT is expressed in J m^{-1} kg^{-1} and s is the walking speed in m s^{-1}.

Here, we present the COT functions for the group:

$$\mathrm{COT}_{\mathrm{floor}} = 2.10s^2 - 5.64s + 6.62, \quad (7)$$

$$\mathrm{COT}_{\mathrm{rough\ terrain}} = 5.67s^2 - 12.76s + 13.54. \quad (8)$$

We found that the average COT values for the rough terrain were approximately 115% greater than those obtained for the smooth floor condition. The preferred walking speed (averaged across all subjects) on rough terrain of 1.07±0.05 m s^{-1} (mean±s.d.) was approximately 14% slower than the preferred walking speed of 1.24±0.17 m s^{-1} on the smooth floor (Fig. 3). The main goal of this study was to compare how humans choose their preferred walking speed on smooth and rough terrain. On both surfaces, the preferred speed was close to the respective energetic optimum speed. The average preferred speed was different between the two surfaces, 1.24±0.17 m s^{-1} on the smooth floor and 1.07±0.05 m s^{-1} on rough terrain (P=0.03). The metabolically optimal average speed (the speed that minimizes the fitted COT functions) was 1.34±0.04 m s^{-1} on the smooth floor and 1.13±0.07 m s^{-1} on rough terrain. For the smooth floor condition, a paired t-test showed no significant difference between the preferred and optimal speeds (P=0.09), whereas for the rough terrain condition,

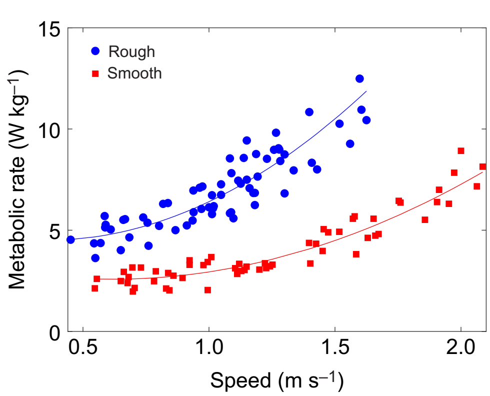

Fig. 2. Metabolic rate as a function of walking speed. Data are from a total of 124 trials (66 trials on rough terrain and 58 trials on smooth floor), obtained from 10 subjects walking at a variety of speeds.

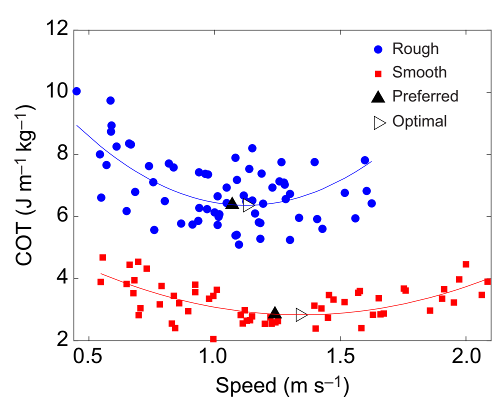

Fig. 3. Cost of transport (COT) as a function of walking speed for all trials. COT values for the rough terrain were approximately 115% greater than those obtained for the smooth floor condition.

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the *t*-test revealed that the preferred speed was significantly slower than the optimal (P=0.02). The values of each subject's preferred and optimal walking speeds are presented in Table 1 and the individuals fits in Appendix 2 (Figs A1 and A2).

COT change as a function of speed

We tested whether the COT versus speed functions differed between the terrain conditions. After normalizing the COT and speed values, we fitted a second-degree polynomial to the COT for each of the two walking surfaces and derived Eqns 9 and 10 for normalized COT:

$$\mathrm{COT}_{\mathrm{norm,floor}} = 1.00 s_{\mathrm{norm}}^2 - 2.18 s_{\mathrm{norm}} + 2.18, \quad (9)$$

$$\mathrm{COT}_{\mathrm{norm,rough\ terrain}} = 1.02 s_{\mathrm{norm}}^2 - 2.14 s_{\mathrm{norm}} + 2.12. \quad (10)$$

where $\mathrm{COT}_{\mathrm{norm}}$ are the COT values of a subject divided by the COT at their preferred speed and s_{norm} is the walking speed of a subject divided by their preferred walking speed. The normalized COT data are shown in Fig. 4. This Chow test also showed a significant difference (P=0.003) between the shapes of the two curves. Yet, the meaningful coefficient (Eqn 4) was only 0.84, which means that the average difference between the model is smaller than the average error in the models predictions. Thus, for the normalized data, although the fitted equations are not the same (Chow test), the normalized COT data for both surfaces show similar behavior as a function of normalized speed.

DISCUSSION

The aim of this study was to compare the preferred speeds and energetic COT for humans walking on smooth and rough terrain. This was achieved by conducting trials across a wide range of walking speeds. The COT for the rough terrain was considerably greater (~115%) than for smooth, level walking, a finding that is very similar to past research for walking on sand (Givoni and Goldman, 1971). The greater COT values for the rough surface likely reflects: greater rates of mechanical work performed on the center of mass and the substrate itself (Lejeune et al., 1998), greater decelerations and accelerations of the center of mass because of foot placement (Kuo et al., 2005; Seethapathi and Srinivasan, 2015), shorter step lengths and wider step widths (Donelan et al., 2001; Zarrugh et al., 1974) and/or other stability-related issues. Voloshina and Ferris (2013) have shown that walking on uneven terrain causes only minor changes in stepping strategy and suggest that the changes in metabolic rate are instead due to a change in the amount of work carried out by lower-limb joints as well as changes in the timing of foot–ground collision and trailing leg push-off.

Table 1. The preferred and optimal walking speeds of each subject on the smooth floor and rough terrain surfaces

Subject number	Preferred speed (m s^{-1})	Optimum speed (m s^{-1})
Smooth floor		
1	1.130	1.357
2	1.054	1.260
3	1.196	1.338
4	1.163	1.346
5	1.240	1.292
6	1.002	1.356
7	1.435	1.356
8	1.164	1.337
9	1.502	1.381
10	1.513	1.366
Average	1.240 (0.173)	1.339 (0.036)
Rough terrain		
1	1.061	1.216
2	1.162	1.159
3	1.037	1.20
4	1.064	1.152
5	1.008	1.057
6	1.131	1.140
7	1.121	1.206
8	1.060	1.015
9	1.033	1.060
10	1.055	1.111
Average	1.073 (0.046)	1.132 (0.068)

The optimal speed value is that which minimized the COT function for each individual subject.

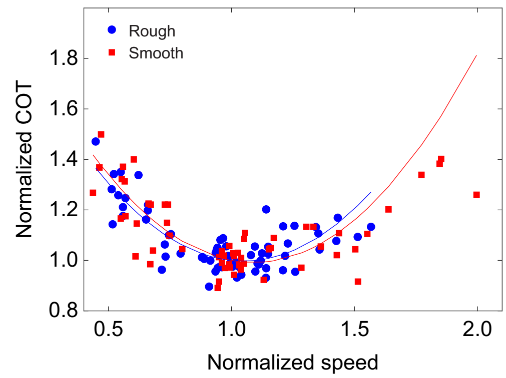

Fig. 4. Comparison of normalized COT functions for the rough terrain and smooth floor conditions

The function describing the dependence of metabolic rate on speed for the smooth, level floor condition in the present study is similar to prediction equations developed in previous studies (Givoni and Goldman, 1971; Ralston, 1958; Zarrugh et al., 1974; Pandolf et al., 1977). Our data for walking on the smooth floor most closely match the prediction equation of Givoni and Goldman (1971) (Fig. 5A). For the rough terrain (Fig. 5B), we compared our data with two prediction equations for metabolic rate from previous studies: Givoni and Goldman (1971) and Pandolf et al. (1977). Both of those studies utilized a terrain factor η that represents the effect of the surface type on metabolic rate. Because we did not know η *a priori*, we used a grid search optimization to calculate the value that minimized the root mean square error (RMSE) between our data and the predictions of both equations. This procedure produced terrain factors of 1.9 and 3.1 for Givoni and Goldman (1971) and Pandolf et al. (1977), respectively. Note that although the Pandolf et al. (1977) equation is used more commonly, the prediction equation of Givoni and Goldman (1971) had the best match to our rough terrain data (lowest RMSE). COT as a function of speed is presented in Fig. 5C,D.

We hypothesized that the objective function for walking speed that humans try to minimize is more complex than just COT and proposed Eqn 1 as one possible form. Specifically, because there was likely to be a difference in stability between the two conditions, we hypothesized that the relationship between preferred speed and the optimal speed (lowest COT) would be different for rough terrain and smooth floor. Our results revealed that, similar to past studies that studied COT on smooth, level ground and treadmills (e.g. Ralston, 1958; Zarrugh et al., 1974), the subjects' preferred speeds on both surfaces were close to the speeds that minimized COT. The preferred speed on the smooth floor was, on average, 8% slower than the optimum speed, but the difference was not statistically significant (P=0.09).

On rough terrain, the preferred speed was 5% slower than the optimum speed (P=0.02). This supports our hypothesis that humans are optimizing a more complex function than

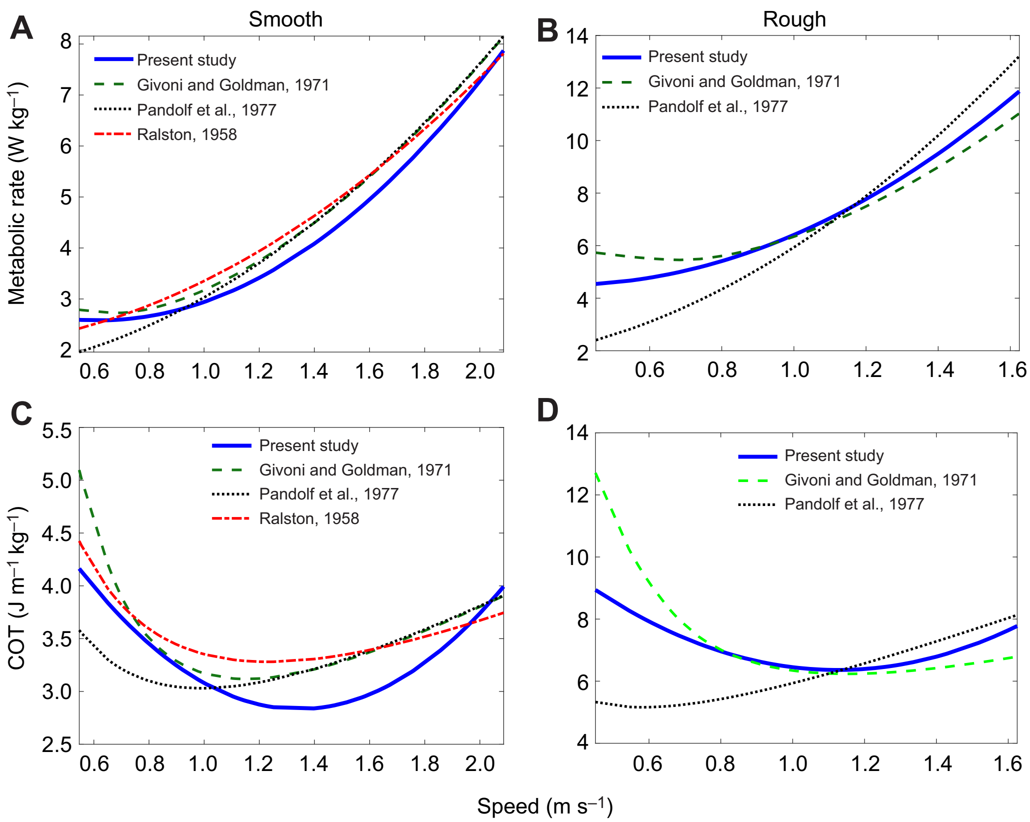

Fig. 5. Comparison of our COT prediction function with those reported previously. Fitted curves of past studies (Ralston, 1958; Givoni and Goldman, 1971; Pandolf et al., 1977) and the present study for metabolic rate (A) and COT (C) for walking on smooth surfaces. Fitted curves to metabolic rate (B) and COT (D) values for rough terrain (present study) and from models that allow for a predictions of COT on different surfaces (Givoni and Goldman, 1971; Pandolf et al., 1977). To learn more about how these curves were generated, see Appendix 3.

$\mathrm{MIN}_{\{\theta\}}[\mathrm{COT}(\theta)]$. We propose Eqn 1 as a possible alternative and argue that when walking on rough terrain, the slower walking speed increases stability, thus reducing the overall value of the objective function. Note that we do not claim that Eqn 1 is the only function possible or that this is the only possible explanation for our results. For example, the slower walking on rough terrain might be due to the need for more accurate foot placement in addition to increased stability (Matthis, Yates, and Hayhoe, 2018). It should also be noted that while everyday experience tells us that slower walking increases stability, we did not model or measure stability on rough terrain as a function of speed.

Compared with the energetically optimal speed, the preferred speed was 8% slower for the smooth floor and 5% slower for the rough terrain. However, the COT functions in Fig. 3 are very shallow near the optimum speed, such that the difference between the preferred speed and optimal speed caused a change in COT value of only 0.8% for the smooth floor and 0.3% for the rough terrain. This indicates that the COT function is relatively insensitive to the change in speed near the optimal COT speed.

Given that our subjects chose to walk at speeds that resulted in a COT only 0.55% greater (on average) than the optimum, it is worth pondering whether humans can sense such a small difference in COT, and if so, how? After all, COT requires information about instantaneous metabolic rate and walking speed. Humans can reliably perceive their physiological effort, presumably via cardiac and pulmonary sensors (Borg, 1982), and their localized effort, which can be reflected in electromyographic recordings (Korol et al., 2014, 2017). More specific to locomotor optimization, Wong et al. (2017) investigated whether people utilize the body's blood gas receptors to identify their optimal step frequency. They experimentally manipulated blood gas (O_2 and CO_2) concentrations and found that their subjects ignored the blood gas receptor information and walked with their normal step frequencies. Another sense that affects the human perception and selection of preferred walking speed is vision (Mohler et al., 2007). Based on this literature, it seems that although humans might prefer certain walking speeds based on instantaneous sensations of effort and speed and thus minimum COT, it is also possible that past walking experience sets the baseline walking speed.

It is worth noting that other species, for example wildebeest (Pennycuick, 1975), elephants (Langman et al., 1995) and horses (Hoyt and Taylor, 1981), also exhibit preferred terrestrial locomotion speeds within each gait. Further, the preferred walking speeds of horses and elephants also are close to their minimum COT speeds (Hoyt and Taylor, 1981; Langman et al., 1995). It remains to be tested whether factors other than COT affect the preferred speeds in these and other species.

In summary, based on both the current findings, which show a difference between the speed that minimizes the COT and the preferred speed on rough terrain, and previous research (Brown et al., 2002; Clark-Carter et al., 1986; Monsch et al., 2012; Schniepp et al., 2014), it seems that simply minimizing COT does not fully represent the human objective function for walking speed. Other walking conditions should be examined to investigate additional parameters that might appear in the cost function, such as stability, reward and time-saving (Summerside, et al., 2018).

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Table A1. Comparison of Bayesian information criterion (BIC) values for polynomial LMM fit for metabolic rate with different orders

Surface	Model polynomial degree	BIC
Smooth floor	1	131.04
	2	64.12
	3	64.30
	4	88.68
Rough terrain	1	161.91
	2	137.65
	3	157.51
	4	176.34

Shading indicates the lowest BIC score.

Table A2. Comparison of BIC values for polynomial LMM fit for COT with different orders

Surface	Model polynomial degree	BIC
Smooth floor	1	108.68
	2	26.59
	3	42.79
	4	66.414
Rough terrain	1	176.23
	2	139.24
	3	157.19
	4	176.36

Shading indicates the lowest BIC score.

APPENDIX 1

The trial speeds and order

There were a total of five speed categories: preferred, very slow, slow, fast and maximum.

The slow speed trials (very slow and slow) were always consecutive, as were the fast speeds (fast and maximum). The maximum speed always came before the fast speed because the fast speed was derived from the maximum speed.

The trial order in the smooth floor sessions was: preferred–X–X–Y–Y–preferred. The trial order in the rough terrain was: preferred–X–X–preferred–Y–Y–preferred. We switched between X and Y (i.e. the fast speeds and the slow speeds) so that half the subjects performed the first sequence while the other half performed the second, to avoid trial order effects. Ergo, there were two sequences for each surface: on smooth floor: (1) preferred–very slow–slow–maximum–fast–preferred, and (2) preferred–maximum–fast–very slow–slow–preferred; and on rough terrain: (1) preferred–very slow–slow–preferred–maximum–fast–preferred, and (2) preferred–maximum–fast–preferred–very slow–slow–preferred.

APPENDIX 2

Consideration for development of the equations

In the past, there have been many forms of equations use to describe the metabolic rate as function of speed (Schertzer and Riemer, 2014; Ralston, 1958; Pandolf et al., 1977). However, the logic for choosing the equation form in these papers is not always clear.

In the present study, in the development of the equation, we used an LMM that allowed us to develop both equations for the average of the population (fixed effect) and also for each individual, where the equation for the individual also takes into consideration the group behavior (Figs A1 and A2). This allowed us to avoid the problem of over-fitting the data (e.g. fitting a third-order polynomial to six data points). We fit our equation to the metabolic rate data and then to COT. We tested the models' goodness of fit using the BIC criteria (Tables A1 and A2). Choosing the right format of the equation is important as we found that in some cases fitting different equations resulted in different speeds that minimize the COT. We also test the fit based on the formulation of Ralston (1958), which used a polynomial fit for metabolic rate, and then divided the metabolic rate equations by the walking speeds to determine the COT [e.g. COT=MR(s)/s]. This was tested using the polynomials of orders 2 to 4, yet BIC values were higher, meaning the fit was worse.

APPENDIX 3

Method of generating COT regression curves using equations from previous studies

In Pandolf et al. (1977), the metabolic rate fitted curve is of the form:

$$\mathrm{MR} = 1.5M + 2(M+L) \times \left(\frac{L}{M}\right)^2 + \eta(M+L) \times (1.5s^2 + 0.35sG), \tag{A1}$$

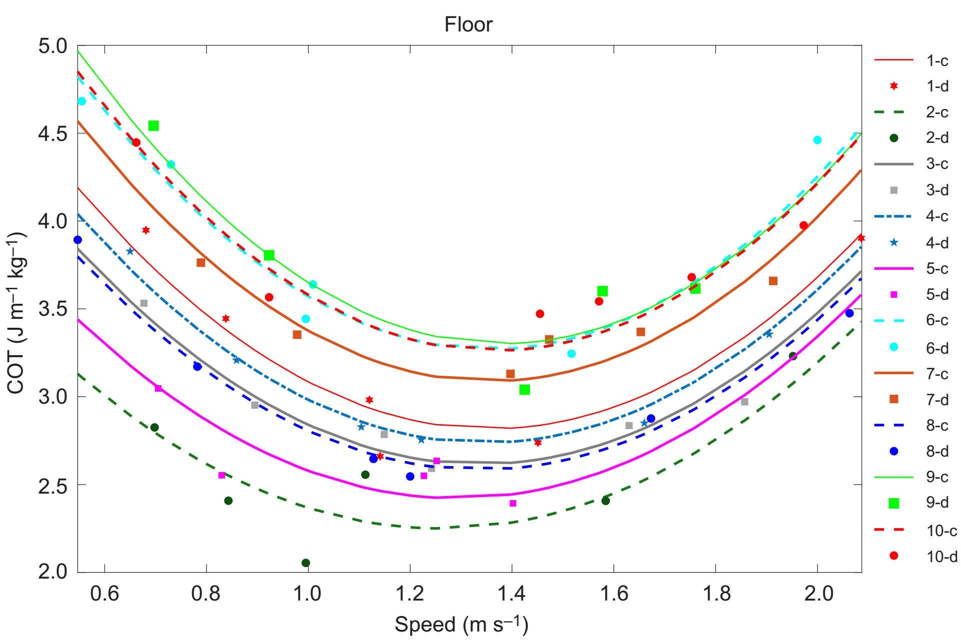

Fig. A1. COT as a function of walking speed for all subjects on the smooth floor condition and the individual models based on the linear mixed model (LMM) method. c, curve fit; d, experimental data.

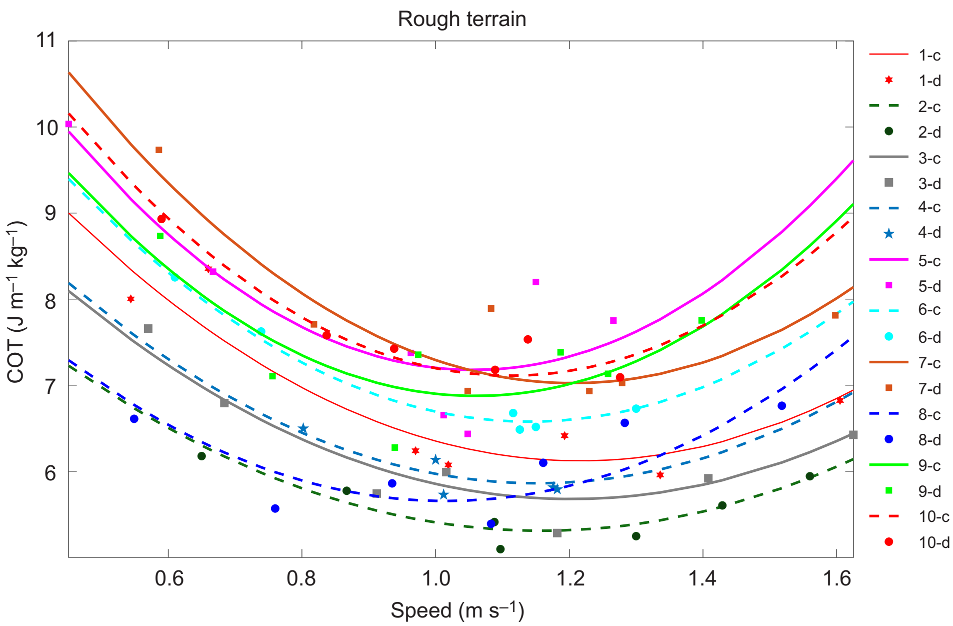

Fig. A2. COT as a function of walking speed for all subjects in the rough terrain condition and the individual models based on the LMM method. c, curve fit; d, experimental data.

where MR is the metabolic rate in watts, M is the body mass (for this study, the average body mass was 76.5 kg) and L is external load, which in our case was 1.5 kg for the metabolic rate measurement system (K4b2, Cosmed). G is the gradient, in our case 0%. η is the terrain factor, and η=1 for smooth floor and η=3.1 for rough terrain, where the latter value was chosen such that it minimized the root mean square error (RMSE) between the experiment best LMM and Pandolf et al.'s (1977) prediction. The walking speed, s, is expressed in m s^{-1}. After assigning the values to equation A1, we obtained:

$$\mathrm{MR_{floor}} = 117s^2 + 114.81, \tag{A2}$$

$$\mathrm{MR_{rough\ terrain}} = 351s^2 + 114.81. \tag{A3}$$

We divided MR by (W+L) to obtain the metabolic rate per kilogram and by s to obtain the COT:

$$\mathrm{COT_{floor}} = 1.50s + \frac{1.47}{s}, \tag{A4}$$

$$\mathrm{COT_{rough\ terrain}} = 4.50s + \frac{1.47}{s}. \tag{A5}$$

In Givoni and Goldman (1971), the metabolic rate regression curve is of the form:

$$MR = \eta \times (M + L) \times \{2.3 + 0.32 \times (s - 2.5)^{1.65} + G \times [0.2 + 0.07(s - 2.5)]\} \tag{A6}$$

where MR is the metabolic rate in kcal h^{-1}, M is the body mass (for this study, the average body mass was 76.5 kg) and L is external load, which in our case is 1.5 kg for the metabolic rate measurement system (K4b2, Cosmed). G is the gradient, in our case 0%. η is the terrain factor, and η=1 for smooth floor and η=1.9 for rough terrain, chosen to minimize the RMSE. In Givoni and Goldman (1971), the walking speed s is expressed in km h^{-1}. After converting to the units used in our study (i.e. m s^{-1} for s and J m^{-1} kg^{-1} for COT) and assigning the above values to Eqn A6, we obtain:

$$\mathrm{MR_{floor}} = 24.96(3.60s - 2.5)^{1.65} + 179.40, \tag{A7}$$

$$\mathrm{MR_{rough\ terrain}} = 47.42(3.6s - 2.5)^{1.65} + 340.86. \tag{A8}$$

We divided MR by (M+L) to obtain the metabolic rate per kilogram and by s to obtain the COT:

$$\mathrm{COT_{floor}} = \frac{0.32(3.60s - 2.5)^{1.65} + 2.30}{s}, \tag{A9}$$

$$\mathrm{COT_{rough\ terrain}} = \frac{0.61(3.60s - 2.5)^{1.65} + 4.37}{s}, \tag{A10}$$

In Ralston (1958), the energy expenditure regression curve is of the form:

$$E_{\mathrm{m}} = \frac{29}{s} + 0.0053s, \tag{A11}$$

where E_{m} is the energy expenditure per unit distance in cal m^{-1} kg^{-1}, and s is the walking speed in m min^{-1}, which needs to be converted to m s^{-1}. After converting to the units used in the present study and assigning the above values to Eqn A11, we obtain:

$$\mathrm{COT_{floor}} = \frac{2.02}{s} + 3.76 \times 10^{-4} \times s. \tag{A12}$$

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Competing interests
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Author contributions
Conceptualization: K.G., R.K., R.R.; Methodology: K.G., R.K., R.R.; Software: K.G., R.R.; Validation: K.G., R.R.; Formal analysis: K.G., R.R.; Investigation: K.G., R.R.; Resources: K.G., R.R.; Data curation: K.G., R.R.; Writing - original draft: K.G., R.R.; Writing - review & editing: K.G., R.K., R.R.; Visualization: K.G., R.R.; Supervision: R.K., R.R.; Project administration: K.G., R.R.; Funding acquisition: R.R.

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