

RESEARCH ARTICLE

Fast and slow processes underlie the selection of both step frequency and walking speed

Renato Pagliara, Mark Snaterse and J. Maxwell Donelan*

ABSTRACT

People prefer gaits that minimize their energetic cost. Research focused on step frequency selection suggests that a fast predictive process and a slower optimization process underlie this energy optimization. Our purpose in this study was to test whether the mechanisms controlling step frequency selection are used more generally to select one of the most relevant characteristics of walking – preferred speed. To accomplish this, we contrasted the dynamic adjustments in speed following perturbations to step frequency against the dynamic adjustments in step frequency following perturbations to speed. Despite the use of different perturbations and contexts, we found that the responses were very similar. In both experiments, subjects responded to perturbations by first rapidly changing their speed or step frequency towards their preferred pattern, and then slowly adjusting their gait to converge onto their preferred pattern. We measured similar response times for both the fast processes (1.4 ± 0.3 versus 2.7 ± 0.6 s) and the slow processes (74.2 ± 25.4 versus 79.7 ± 20.2 s). We also found that the fast process, although quite variable in amplitude, dominated the adjustments in both speed and step frequency. These distinct but complementary experiments demonstrate that people appear to rely heavily on prediction to rapidly select the most relevant aspects of their preferred gait and then gradually fine-tune that selection, perhaps using direct optimization of energetic cost.

KEY WORDS: Gait, Biomechanics, Neuromechanics, Motor control, Energy optimization

INTRODUCTION

Beginning with the work of Ralston in the 1950s, researchers have repeatedly shown that the preferred characteristics of walking – including speed, step frequency and step width – minimize energetic cost (Bertram, 2005; Bertram and Ruina, 2001; Donelan et al., 2001; Elftman, 1966; Ralston, 1958). Recently, researchers from our laboratory have attempted to elucidate the mechanisms through which the human body selects these energetically optimal patterns. Our focus to date has been primarily on the selection of step frequency because it is a general characteristic of locomotion that can be readily manipulated and measured, it has a strong effect on energetic cost and its selection appears to be highly optimized (Minetti et al., 1995; Snaterse et al., 2011; Snyder et al., 2012; Umberger and Martin, 2007). Our approach has been to treat the human body as a dynamic system that selects energetically optimal gaits using internal processes that can be examined by providing controlled inputs to the system and measuring the system's dynamic response. For example, we have

previously used rapid changes to treadmill speed as the controlled inputs to treadmill walking and measured the resulting transient adjustments of step frequency towards the new preferred value at each speed (Snaterse et al., 2011).

This work has shown that two distinct processes acting over different timescales appear to underlie the selection of preferred step frequency during treadmill walking (Fig. 1). One process is very fast, acting to quickly bring step frequency towards its energetically optimal value within the first few steps following a change in walking speed (Snaterse et al., 2011). This response time is too rapid to involve direct sensing of metabolic cost, indicating that the process must rely on indirect feedback and prior experience to predict energetically optimal step frequencies (Snaterse et al., 2011). The second slower process, responsible for the remainder of the change in step frequency, may use direct measures of metabolic cost to fine-tune step frequency to its energetically optimal value (Snaterse et al., 2011). Subsequent experiments have demonstrated that fast and slow processes also underlie step frequency adjustments in human running, indicating that they are fundamental strategies for selecting energetically optimal step frequencies (Snyder et al., 2012). Selecting step frequency by combining the rapidity of prediction with the accuracy of optimization appears to be a sensible strategy. Using prediction alone would be inaccurate, especially in unfamiliar or unknown contexts, whereas using optimization alone would be too slow to make energetically optimal adjustments in changing conditions. Although this combination may be a sensible strategy for selecting any characteristic of gait that has a meaningful energetic cost, the above evidence is specific to step frequency selection.

Recent work by O'Connor and Donelan (O'Connor and Donelan, 2012) tentatively suggests that the same fast prediction and slow optimization processes may underlie the control of walking speed. The authors applied visual perturbations to subjects walking on a self-paced treadmill to convey a visual perception of suddenly walking much slower or faster than their normally preferred speed. Subjects first rapidly adjusted their walking speed in response to the perturbation to bring the visually perceived speed closer to their preferred speed. They then slowly returned to their preferred, and presumably energetically optimal, walking speed. Although these results are suggestive, it is, unfortunately, not possible to directly compare these findings with those of the previous step frequency selection experiments. The visual changes perturbed only one of potentially many inputs into the prediction process, affecting the magnitude of its contribution and perhaps its timing. Also, subjects were free to adjust both their speed and step frequency simultaneously, making it difficult to test whether speed is independently controlled in the same way as step frequency.

Our purpose in this study was to determine whether the selection of preferred step frequency and preferred speed are governed by the same control mechanisms. To accomplish this, we perturbed subjects' gait during two distinct but complementary walking

Department of Biomedical Physiology and Kinesiology, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

*Author for correspondence (mdonelan@sfu.ca)

Received 17 March 2014; Accepted 22 May 2014

List of symbols and abbreviations

A	amplitude
GPS	global positioning system
r.m.s.	root mean square
T_d	physiological time delay
$X(s)$	model input
$Y(s)$	model output
τ	time constant

List of subscripts

f	fast
s	slow

experiments and observed the transient adjustments in gait towards their preferred pattern. The first experiment studied the dynamics of step frequency selection in response to speed perturbations during treadmill walking. The second experiment studied the dynamics of speed selection in response to step frequency perturbations during overground walking. We used numerical optimization techniques to identify the number of processes involved in the observed gait adjustments, as well as the best-fit timing parameters for each process. To test whether fast and slow processes underlie the selection of both step frequency and speed, we compared the number of processes, and the timing of each process, identified in the two experiments.

RESULTS

We found that fast and slow processes appear to govern the selection of both preferred step frequency and preferred speed. In both experiments, subjects responded to perturbations by first rapidly changing their gait towards their preferred pattern and then slowly fine-tuning their gait to settle on their steady state value (Fig. 2). These dynamics were captured by the sum of a fast and slow process (Eqn 1) with the two processes having large and significant differences in their response times. Specifically, the fast and slow processes underlying frequency selection during the speed perturbation experiments had respective response times of 1.4 ± 0.3 and 74.2 ± 25.4 s (mean \pm s.d.; $P=8.38 \times 10^{-5}$ paired t -test). Similarly, speed selection fast and slow response times were 2.7 ± 0.6 and 79.7 ± 20.2 s ($P=1.16 \times 10^{-5}$) during the frequency perturbation experiments. Comparing response times between experiments, the fast process values were similar in magnitude but nevertheless

statistically different ($P=3.2 \times 10^{-3}$). The slow response times were not significantly different ($P=0.69$). Subjects also exhibited delays of similar magnitude prior to responding to the perturbations with a median (interquartile range) delay of 0.1 (0.2 s) for frequency changes in response to speed perturbations and 0.3 (0.5 s) for speed changes in response to frequency perturbations ($P=8.22 \times 10^{-10}$).

The fast process dominated the measured adjustments in both step frequency and walking speed. On average, the fast process amplitude was very close to 1 (1.02 ± 0.04 and 0.96 ± 0.08 for speed and frequency perturbation experiments, respectively), whereas the slow process amplitude was very close to 0 (-0.02 ± 0.04 and 0.04 ± 0.08 for speed and frequency perturbation experiments, respectively). Thus, on average, the fast process rapidly and accurately adjusted gait towards the final steady state value requiring small fine-tuning adjustments from the slow process. However, this average response does not accurately convey how the relative contributions of the two processes varied from trial to trial (Fig. 3). For example, the fast process amplitude varied between 0.76 and 1.34 when selecting frequency in the speed perturbation trials, and between 0.57 and 1.38 when selecting speed in the frequency perturbation trials (95% confidence intervals). Fast process amplitudes greater than 1 indicate initial adjustments that overshoot the final steady state value, whereas those less than 1 indicate initial responses that undershot the steady state value. In both ‘fast overshoot’ and ‘fast undershoot’ trials, the slow process contributed the remaining adjustments to slowly converge the subject to steady state. In some trials, the initial response did not overshoot or undershoot but brought the subject very close to the preferred steady state gait yielding a fast process amplitude close to 1. In these ‘fast accurate’ trials, defined here as A_f between 0.95 and 1.05, the contribution of the slow process was small compared with the step-to-step variability in step frequency or speed. In the speed perturbation experiment, 33% of the frequency responses were fast undershoot, 32% were fast overshoot and 35% were fast accurate. In the frequency perturbation experiments, 49% of the speed responses were fast undershoot, 31% were fast overshoot and 20% were fast accurate. The only effect of perturbation direction and magnitude on the initial responses in the two experiments that we found was that subjects were more likely to undershoot in the speed perturbation experiments when the perturbation consisted of an increase in belt speed ($P=0.005$, chi-square test).

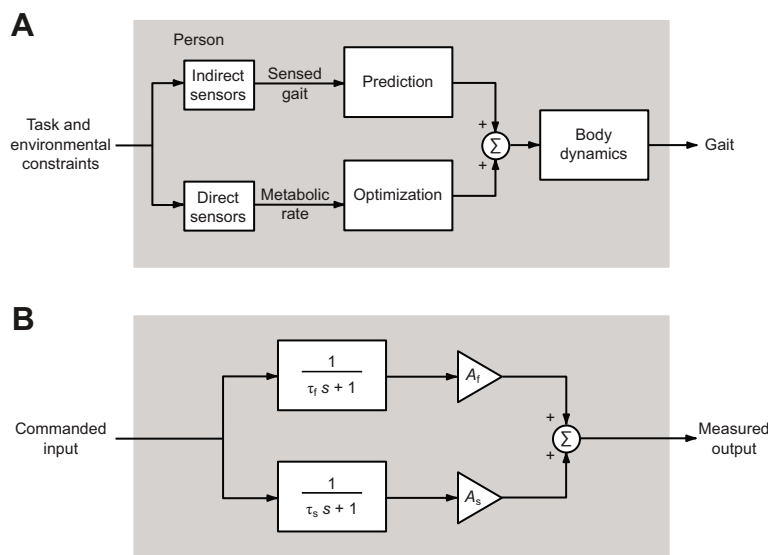


Fig. 1. Two-process model of gait selection. Based on previous research (O'Connor and Donelan, 2012; Snerse et al., 2011; Snyder et al., 2012), we treat the person as a dynamic system that uses internal processes to select the energetically optimal gait for a particular task under particular environmental constraints. These processes can be examined by providing controlled inputs to the system and measuring the system's dynamic response. (A) Based on our previous findings, we theorize that a combination of two physiological processes operating on different time scales work in parallel to select energetically optimal walking parameters. One of these processes acts very quickly and is believed to reflect a predictive process that relies on previous experience and indirect sensors of energetic cost, such as vision, to quickly select economical gaits. The second process, acting much slower, is believed to reflect an optimization process that uses sensed metabolic rate directly to minimize energetic cost. The resulting gait is the product of these fast and slow processes applied to the body's own task-dependent dynamics. (B) We mathematically modelled these fast and slow dynamics using two parallel first-order processes with variable amplitudes. For a step input, the resulting output is the sum of two exponential functions that work together to converge the system to a steady state.

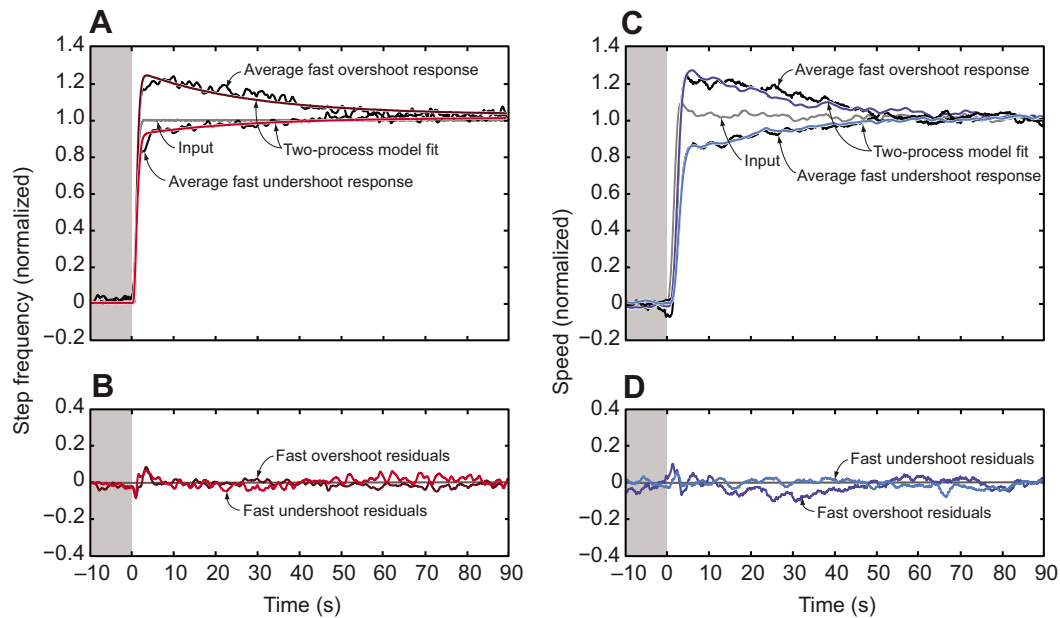


Fig. 2. Results. (A,B) Speed perturbation experiments. (A) A rapid change in treadmill speed elicited rapid adjustments in step frequency followed by longer-term adjustments towards the new steady state value. The initial rapid adjustment varied from trial to trial, sometimes undershooting or overshooting the final steady state value. We fitted a two-process model (red and burgundy lines) to the average normalized fast-undershoot and fast-overshoot experimental data (black lines), using the treadmill speed (grey line) as the input to the system. (B) The residual errors between the model and the experimental data illustrate that the two-process model was sufficient to describe the dynamics in step frequency selection – the residuals were small and approximately randomly distributed around 0. (C,D) Frequency perturbation experiments. (C) A rapid change in metronome frequency elicited a rapid adjustment in walking speed followed by longer-term adjustments towards the new steady state speed. (D) The residual errors illustrate that the same two-process model yields fits that closely match the speed response experimental data, suggesting that the two-process model is also sufficient to explain the dynamics behind the selection of walking speed. To compare trials with different perturbation magnitudes and directions, as well as across experiments, we normalized the data of each trial to yield a magnitude of 0 prior to the perturbation and a magnitude of 1 at the final steady state value. In all panels, the grey area indicates the time prior to the perturbation.

The two-process model accurately described the measured response to perturbations in both experiments. R^2 values for individual trial fits indicate that the model explained $53 \pm 16\%$ and $68 \pm 10\%$ of the measured variance for the speed and frequency perturbation experiments, respectively. These are respectable fits given that the model does not attempt to explain the variability

present during steady state walking in both step frequency and speed. We estimated the contribution of this steady state behaviour to the total adjustments in gait for each trial from the average variance in the 10 seconds immediately before each perturbation and in the final 10 seconds of the trial. It was relatively large, accounting for $29 \pm 20\%$ and $17 \pm 15\%$ of the adjustments in step frequency and

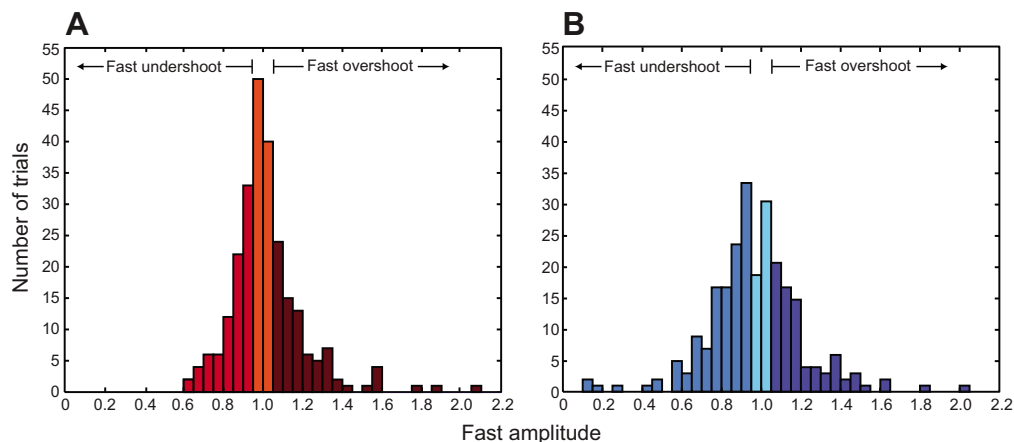


Fig. 3. Fast process amplitude distribution for all subjects and all trials. The distribution of the fast process amplitude (A_f) is shown for the speed perturbation experiments (A) and frequency perturbation experiments (B). Our analysis approach normalized the steady state frequency and speed of each trial to 1. That the illustrated distributions are both centered around 1 indicates that, on average, the fast process brought both step frequency and speed very close to their final steady state values. However, the contribution of the fast process to the overall response varied considerably from trial to trial, as indicated by the spread of the distributions. We classified trials with a fast amplitude less than 0.95 as fast undershoot, trials with a fast amplitude greater than 1.05 as fast overshoot and trials with fast amplitude between 0.95 and 1.05 as fast accurate. Because the amplitudes of the fast and slow processes were defined to sum to 1, the greater the deviation of the fast process amplitude from 1, the larger the contribution of the slow process to the overall response.

speed, respectively. To further test the two-process model, we determined how well the average response times from the individual fits described the average perturbation responses. This averaging reduced the contribution of steady state variability to the measured adjustments because, from trial to trial, the steady state adjustments were uncorrelated with perturbation onsets. For this purpose, we only used the average fast undershoot ($A_f < 0.95$) and fast overshoot ($A_f > 1.05$) trials because the fast accurate trials did not contain a measurable slow process. The R^2 values for the frequency response in the speed perturbation trials indicate that the model explained 96% and 95% of the average fast undershoot and fast overshoot responses, respectively (Fig. 2A). Similarly, the R^2 values for the speed response in the frequency perturbation trials indicate that the model explained 99% of the average fast undershoot responses and 96% of the average fast overshoot responses (Fig. 2C). Furthermore, the residual errors were small and showed no clear pattern (Fig. 2B,D). Collectively, these results indicate that the two-process model provides a good explanation of the dynamics of both walking speed and step frequency selection.

A comparison with simpler and more complex models suggests that the two-process model is both necessary and sufficient to describe the measured responses to perturbations. A simpler one-process model is not sufficient, as it cannot mathematically account for the substantial overshooting behaviour that was present in approximately one third of the trials from both experiments (Figs 2, 3). Furthermore, a single process cannot capture both the rapid initial adjustments in gait as well as the slower fine-tuning (Fig. 2). Although these are not limitations for a more complex model, the added complexity does not seem warranted given how well the two-process model performed. The residual errors between the average measured data and the model predictions (Fig. 2B,D) are quite small and appear to be randomly distributed about 0, indicating that a two-process model leaves very little remaining variability to be explained by additional processes in more complex models.

DISCUSSION

The two processes that appear to govern the selection of step frequency are remarkably similar to those that seem to control walking speed. The faster of the two processes rapidly adjusts frequency and speed, bringing people towards their preferred gait within a few steps. The slower process takes considerably longer, fine-tuning speed and frequency to slowly converge people to their energetically effective steady state gait. We consistently observed these processes despite major differences between our two experimental paradigms – we studied frequency selection in experiments that took place on a treadmill and physically perturbed speed, and speed selection in experiments that applied nonphysical perturbations to overground walking. In previous running experiments we found that similar fast and slow processes appear to govern step frequency selection as those described here in walking, even though distinct biomechanical mechanisms underlie the two gaits (Cavagna et al., 1976; Snyder et al., 2012). These collective findings strongly suggest that these two processes reflect common control mechanisms for selecting preferred gait patterns.

The identified dynamics were similar between the two experiments, but not identical. Differences are expected even when identical neural mechanisms are responsible for selecting speed and frequency because the body has its own dynamics and these dynamics depend upon the particular task (Fig. 1). For a given input, speed changes are likely to occur more slowly than step frequency changes because the former involves the acceleration of the mass of the whole body, whereas the latter mostly requires the acceleration

of the mass of one leg. This provides one reasonable explanation as to why the identified fast process was statistically faster in the speed perturbation experiments when compared with the frequency perturbation experiments. Although subjects also had to adjust speed in the speed perturbation experiments, and frequency in the frequency perturbation experiments, these adjustments were enforced by the experimental paradigm and were not governed by the dynamics of the neural control underlying the selection of preferred gait. Differences in body dynamic responses are expected to have a smaller effect on longer-term adjustments to gait because the required accelerations are much smaller – we found no significant differences in the dynamics of the two slow processes. A second explanation for identifying a more rapid fast process when selecting frequency is that the treadmill physically perturbed participants with forces that may have also accelerated step frequency towards the preferred value for the new speed. More generally, although our focus is on studying the nature of the underlying control, our measurements do not dissociate neural responses from those that are biomechanical. Hence, all inferences regarding the underlying control should be made in the light of the complete neuromechanical system – small differences in the timing of processes between experiments should not be interpreted as differences in the underlying neural control.

Although we have examined how step frequency is selected in one of our experiments, and how speed is selected in the other, we could have studied how step length is selected in both experiments. Owing to the relationship between speed, step frequency and step length, step length can be defined as speed divided by step frequency. That is, subjects were also selecting a step length when they were selecting a frequency or a speed. The amplitudes of the step length dynamic responses would be opposite to that observed for the other free variable. For example, if step frequency initially undershoots steady state in a speed perturbation trial, step length would overshoot. But while the amplitudes are opposite, the timing of step length selection would exactly match that of the other gait variable that was free to vary. Thus, our central finding that two similar processes govern gait selection in the two experimental models would remain the same had we focused our analysis on step length. When viewed through the lens of step length selection, the central finding is no less remarkable because the two experiments present different challenges to the mechanisms underlying gait selection. In one experiment, the task is to select the optimal gait at a given speed, and for the other, it is to select the optimal gait at a given frequency. Step length analyses lead to the same conclusions – people choose their energetically optimal gait by combining a fast selection process with a slow one.

Prediction and optimization of energetic cost remain reasonable candidate control mechanisms responsible for the observed fast and slow processes. Direct optimization of energetic cost is likely to be a slow process due not only to the lengthy feedback delays associated with direct sensing of muscle energetic cost (Coote et al., 1971; Hayes et al., 2009; Kaufman and Hayes, 2002; Kaufman et al., 1983; McCloskey and Mitchell, 1972), but also to the nature of optimization. That is, optimization requires averaging energetic measurements over a number of strides and iteratively adjusting gait parameters to slowly and accurately converge on the optimal gait. This suggests that direct optimization will take tens of seconds or longer. This timing may be consistent with the observed slow process dynamics but far too slow to be responsible for the rapid fast process adjustments. Consequently, we have previously attributed the fast process to the rapid prediction of the energetically optimal walking pattern, based not on direct feedback of energetic cost, but on prior knowledge of the relationship

between gait patterns and energetic cost (Snaterse et al., 2011). Our current results indicate that the sensible strategy of combining the quickness of prediction with the accuracy of optimization is not only used for step frequency selection, but also for the real-time selection of energetically optimal speed.

The fast process adjustments in our experiments were very fast, but not very accurate (Fig. 3). We found considerable variability from trial-to-trial in how closely the fast process amplitude approximated the final steady state value. For example, there were cases where the same subject in the same condition would considerably undershoot the steady state value in one trial and considerably overshoot in another. Two requirements need to be met to allow the fast process to accurately adjust gait. First, the current walking state has to be estimated accurately. Second, the predictive process has to accurately predict the optimal gait adjustments given this estimated state. Inaccuracies in either the state estimate or predictive process would lead to inaccurate gait adjustments. We believe that the inaccuracies in the fast gait adjustments found here might be the consequence of inaccurate estimates of state, as opposed to inaccuracies in the predictive process. Because our perturbations were designed to be unpredictable in both timing and magnitude, the nature of our experiments required subjects to make a hasty, and perhaps imprecise, assessment of their new state. In contrast, many adjustments that are made in the real world are due either to anticipated external perturbations, such as when one steps on to a moving escalator (Reynolds and Bronstein, 2003), or to internally generated perturbations, such as when one decides to walk faster. Our finding that the fast process was quite accurate on average is consistent with the possibility that an accurate predictive mechanism, based on an inaccurate estimate of state, is responsible for our observed fast process inaccuracies. Participants were, on average, within $2\pm 4\%$ and $4\pm 8\%$ of the steady state frequency and speed in just a few steps. And although there were certainly some trials where the initial adjustments were a quite poor prediction of the final steady state value, there were zero trials in which the initial adjustments were not in the correct direction. That is, there was always an energetic saving as a result of the fast predictive adjustments. An alternative possibility for the fast process inaccuracy is that the remaining energetic penalty is simply not enough to justify the additional neural overhead of accurate prediction when optimization will eventually bring the gait to its energetic optimum. We suspect that this is not the correct explanation because perturbations in the real world can come much more frequently than those applied here. In these situations, optimization will not have time to bring the gait to its optimal value creating a persistent, and probably meaningful, energetic penalty if prediction is consistently poor.

Real-time optimization is a viable strategy for the selection of only a relatively small number of gait parameters. Consider, for example, that selecting energetically optimal high-level parameters, such as speed and step frequency, requires the appropriate control of tens of thousands of motor units. The time required to find the optimal combination of parameters is likely to grow quickly with the number of independent parameters. This is because the central nervous system will have to evaluate the effect of a change in each parameter on energetic cost in order to intelligently search the parameter space. But most walking bouts are relatively short, lasting less than 30 seconds (Orendurff et al., 2008), leaving little time for multidimensional optimization. Thus, it seems reasonable that real-time optimization is reserved for a small number of gait parameters that have the most meaningful short-term effects on energetic cost and that are free to change while still fulfilling the task constraints.

Remaining parameters, which may include some high-level parameters (e.g. trunk angle) in addition to low-level parameters (e.g. motor unit activation), must then be predicted based on prior experience acquired over time.

Our results provide further evidence that when walking, people are not predicting and optimizing energy cost per unit time. In our speed perturbation experiments, gait adjustments that minimized the metabolic energy cost per unit distance (i.e. cost of transport) were identical to those that minimized the cost per unit time (i.e. metabolic power) because each new speed was fixed. It is thus impossible from those experiments alone to discriminate which of these two energetic objective functions are predicted and optimized during walking. This is not the case in our frequency perturbation experiments where minimizing metabolic power yielded specific predictions about preferred gaits, and these predictions differ from those of minimizing cost of transport. For any of our experimentally fixed step frequencies, walking with the shortest possible step length, and thus the slowest possible speed, would have minimized metabolic power (Donelan et al., 2002). Yet, our subjects did not show a systematic convergence to very slow walking. In fact, they chose to increase their speed when presented with a higher step frequency, and this speed increase was accomplished not just by fulfilling the enforced frequency but also by increasing step length (on average, step length accounted for 24% of adjustments to speed in our frequency perturbation experiments, with step frequency contributing the remainder). This behaviour is consistent with optimizing cost of transport, which is minimized at a specific non-zero walking speed for each step frequency (Bertram, 2005; Donelan et al., 2001). There is a large body of evidence that convincingly demonstrates that people's preferred steady state gait minimizes cost of transport (Bertram, 2005; Bertram and Ruina, 2001; Donelan et al., 2001; Elftman, 1966; Ralston, 1958) – this study contributes to our understanding by studying the real-time dynamics of this energetic preference.

There were a number of important limitations to our study. First, we used treadmill speed, rather than actual subject speed, as the input into the parameter identification procedure for our speed perturbation experiments. However, subjects can temporarily use different speeds from the treadmill speed by allowing themselves to move backwards or forwards on the belt. Although this is likely to be a small effect – the speeds cannot differ by much or for very long without the subject falling off the belt – it would nevertheless have been more accurate to have measured and used the actual speed. This was not an issue in the frequency perturbation experiments where we used the measured step frequency, rather than the instructed step frequency, as the input. Second, we did not randomize the order in which subjects performed the experiments – all subjects performed the speed perturbation experiments before the frequency perturbation experiments. Although the two experiments were performed in different settings, it would have been more cautious to randomize the order so as to reduce the familiarity of subjects with the experimental protocol. A third limitation is the accuracy of the parameters identified for our fast and slow processes. The specific values depend on many details, including the experimental design we used to generate the input data, the assumptions we made regarding the underlying system and the optimization process we used to identify the best-fit system parameters. We have been refining our approach over the course of our research in this area (O'Connor and Donelan, 2012; Snaterse et al., 2011; Snyder et al., 2012). Consequently, there are important differences between the various approaches that render a detailed quantitative comparison of system parameters between experiments

useless. This same limitation can also be viewed as a strength – despite numerous differences between our approaches, we have consistently found that the selection of preferred gait patterns are governed by two distinct processes that operate on very different time scales. Fourth, although we tried to strike the best balance between the duration of each trial, the total number of trials and the total duration of each experimental session, trial duration was probably too short for some subjects. This is because the normalization of the data from each trial assumes that the subject has reached steady state in the last 30 seconds of each trial. But for subjects with particularly slow dynamics, this assumption would be approximate at best and result in an artificial reduction in our estimates of their slow process time constant. Finally, we interpret our findings in the context of energy minimization, but without directly measuring metabolic cost. Instead, we have relied on previous research by a number of different investigators, using a variety of experimental protocols, which have all demonstrated that the preferred steady state step frequency and speed minimizes metabolic cost (Bertram, 2005; Bertram and Ruina, 2001; Donelan et al., 2001; Elftman, 1966; Ralston, 1958).

In summary, people appear to rely on two distinct processes to select their energetically optimal gaits. They use a fast predictive process to rapidly select their preferred gait and then gradually fine-tune that selection over a time course consistent with direct optimization of energetic cost. These processes underlie gait selection in both walking and running, and in selecting both preferred step frequency and preferred speed, suggesting that they may be general physiological mechanisms for energy optimization. This combination of prediction and optimization has a clear energetic advantage over using either in isolation, in that they can combine to quickly adjust gait during short and varying bouts of locomotion while still being able to find energetically optimal gaits in new contexts.

MATERIALS AND METHODS

Eight healthy young adults (four men, four women; age 24 ± 2 years; leg length 0.82 ± 0.03 m; mean \pm s.d.) participated in our study. Each individual participated for 2 days, with no more than 2 hours of walking per day. They performed the speed perturbation experiments on the first day and the frequency perturbation experiments on the second day. Simon Fraser University's Office of Research Ethics approved the protocol, and participants gave their written informed consent before experimentation. We familiarized the subjects with all procedures prior to the experiments.

Speed perturbation experiments

We applied speed perturbations to subjects walking on a treadmill using rapid changes in belt speed and observed the resulting adjustments in step frequency (Fig. 4A). The perturbations were intended to force subjects to quickly change their speed while at the same time providing considerable freedom in the time course of their adjustments to step frequency, so long as step length was also adjusted to match the appropriate speed. When speed is constrained, subjects cannot independently vary step length and frequency – step length is defined as speed divided by step frequency. Here, we used the convention of referring only to step frequency or speed selection, with the understanding that step length is also being selected, albeit not independently of the other two gait parameters. This protocol used two base speeds: 1.0 and 1.5 m s^{-1} . At each base speed, we applied a series of eight speed perturbations to and from new speeds that were 25% and 50% above and below the base speed (Fig. 4B). Each new speed was maintained for 90 seconds. Subjects repeated each series of perturbations, at each base speed, twice. Series order, and order of the perturbations within a series, were randomized.

This experiment was performed on an instrumented treadmill (FIT, Bertec Corporation, Columbus, OH, USA), allowing us to compute step frequency from the time derivative of the centre of pressure signal in the fore–aft direction (Verkerke et al., 2005). Custom written software (Simulink Real-Time Workshop, MathWorks Inc., Natick, MA, USA) controlled the treadmill speed while an optical encoder mounted on the belt roller measured actual treadmill speed. We chose the maximum belt acceleration (± 0.4 m s^{-2}) to be considerably lower than that normally used

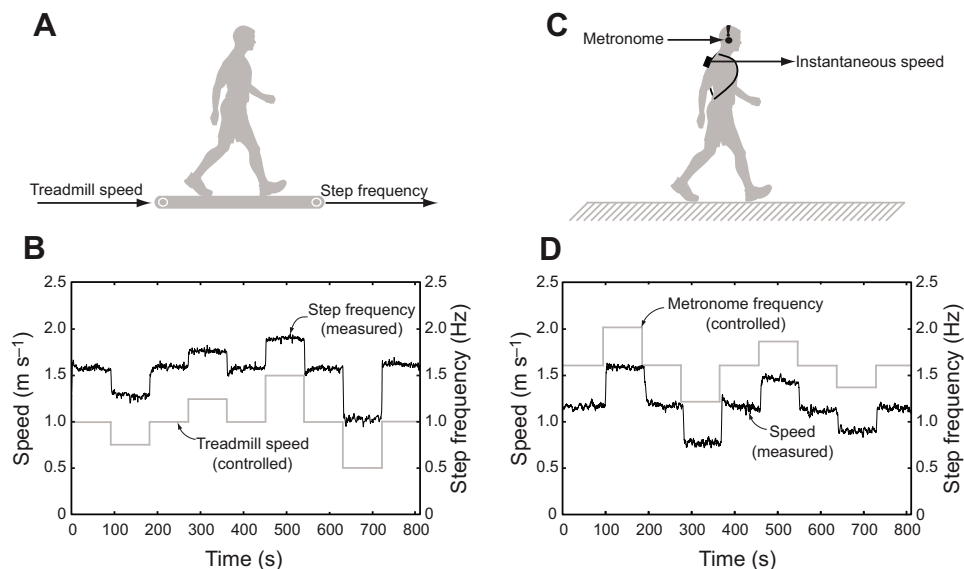


Fig. 4. Experimental methodology. (A) In the speed perturbation experiments, subjects walked on an instrumented treadmill that allowed us to control speed and measure step frequency. (B) We perturbed subjects with rapid changes in treadmill speed of magnitudes 25% and 50% from and to a base speed, forcing subjects to quickly adjust their walking speed while allowing them to freely adjust their step frequency over any time course. Speed was held constant for 90 seconds between perturbations. The data illustrated here is from one series of perturbations by a single subject at a base speed of 1.0 m s^{-1} . (C) In the frequency perturbation experiments, subjects walked overground while synchronizing their steps to a metronome. We measured walking speed using a GPS-based speed sensor, carried by the subjects on a small backpack. (D) We perturbed subjects with rapid changes in metronome frequency of magnitudes 15% and 30% to and from a base frequency, forcing subjects to quickly adjust their step frequency while allowing them to freely adjust their walking speed over any time course. Between perturbations metronome frequency was held constant for 90 s. The data illustrated here are from one series of perturbations by a single subject at a base step frequency equal to their preferred frequency when walking at 1.0 m s^{-1} .

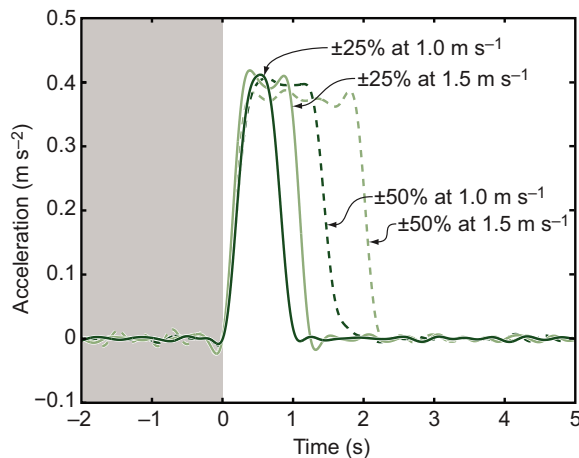


Fig. 5. Average treadmill belt acceleration during the speed perturbation experiments. The experimental protocol for the speed perturbation experiments used two base speeds: 1.0 m s^{-1} (dark green) and 1.5 m s^{-1} (light green). At each base speed, we applied perturbations to and from new speeds that were 25% (solid lines) and 50% (dotted lines) above and below the base speed. The maximum belt acceleration was $\pm 0.4 \text{ m s}^{-2}$, resulting in speed changes lasting from 1.0 to 2.2 seconds.

to challenge balance by eliciting stumbling reaction reflexes (Dietz et al., 1987) while still producing relatively sudden changes in speed. The constant maximum belt acceleration combined with different magnitudes of speed perturbations resulted in speed changes lasting from 1.0 to 2.2 seconds (Fig. 5).

Frequency perturbation experiments

We applied frequency perturbations consisting of rapid changes in metronome frequency to subjects walking overground and observed the resulting adjustments in walking speed (Fig. 4C). The perturbations required subjects to quickly change their step frequency but allowed them to adjust their walking speed over any time course. They were not intended to challenge balance, and subjects could comfortably make the commanded step frequency adjustments. Similar to the speed perturbation protocol, subjects completed a total of four series of perturbations referenced to two different base frequencies. We defined the base frequencies as the subject's preferred step frequencies at speeds of 1.0 and 1.5 m s^{-1} , as measured during the speed perturbation experiments. These subject-specific frequencies averaged 1.6 Hz at 1.0 m s^{-1} and 1.9 Hz at 1.5 m s^{-1} . Each series consisted of eight frequency perturbations to frequencies 15% and 30% above and below the base frequency (Fig. 4D). Each new frequency was maintained for 90 seconds. Series order, and order of the perturbations within a series, were randomized. Participants were explicitly instructed to match their steps to the auditory metronome, and a *post hoc* analysis indicated that they did so accurately. The steady state and root mean square (r.m.s.) errors in step frequency, averaged across subjects, were $0.88 \pm 0.91\%$ and $2.37 \pm 0.83\%$, respectively.

The frequency perturbation experiments were performed on a standard 400 m athletic track (IAAF, 2008). To measure step frequency, we used force-sensitive resistors mounted below the subject's heel. To measure walking speed, we used a global positioning system (GPS) sensor designed for high-accuracy speed sensing (VBOX Speed Sensor, Racelogic, Buckingham, UK; 10 Hz sampling frequency; 43 ms time delay). We validated the accuracy of the sensor by comparing its performance over a wide range of walking speeds and accelerations to that of a wheel instrumented with an optical encoder. The average and r.m.s. error were -0.2% and 2% , respectively. An Arduino UNO microcontroller board (Arduino, Ivrea, Italy) logged the data to a Secure Digital card while a second microcontroller generated the metronome frequency. We mounted both the speed sensor and the microcontroller boards to a lightweight backpack that the subjects wore during the experiment (total mass: 1.5 kg).

Data analysis

For both experiments, we divided each series of perturbations into individual speed or frequency perturbations and their corresponding frequency or speed responses. We refer to these input–output pairs as trials. To compare trials between the speed and frequency perturbation experiments, and to also compare trials of different perturbation magnitudes and directions from within the same experiment, we normalized the input and output data to 0 before the perturbation and 1 after the perturbation. We defined 0 as the average of the 30 seconds of data immediately prior to the perturbation (seconds -30 to 0) and 1 as the average of the trial's last 30 seconds of data (seconds 60 to 90).

We primarily focused on the following two-process system, expressed in the frequency domain, to model the dynamics involved in the selection of gait parameters:

$$Y(s) = \left[\left(\frac{A_f}{\tau_f s + 1} \right) + \left(\frac{A_s}{\tau_s s + 1} \right) \right] e^{-T_d s} X(s), \quad (1)$$

where $X(s)$ is the input and $Y(s)$ is the output. The parameters τ_f and τ_s represent the time constants of the fast and slow processes. The parameters A_f and A_s represent the amplitudes of the fast and slow processes, which we use to determine their relative contributions. We constrained the amplitudes to sum to 1 by enforcing $A_s = 1 - A_f$. The parameter T_d is a time delay to account for physiological time delays. The behaviour of this two-process system is perhaps most easily visualized when the input is an instantaneous step function – the output is then the sum of two exponential functions, one that converges to steady state quickly and one that converges to steady state slowly (Snaterse et al., 2011; Snyder et al., 2012). For convenience, we report time constants as response times, defined as the time required to reach 95% of the final value of the process (approximately three time constants).

For each subject, we independently determined the optimal model parameters for each of the two experiments. During the optimization of each experiment, we assumed that the timing of the fast and slow processes would be the same across all trials for a given individual and thus searched for a single pair of fast and slow process time constants that best fit the entire dataset. As we expected the contribution of the two processes to vary from trial to trial (Snyder et al., 2012), we allowed processes to have different best-fit amplitudes between trials.

We estimated model parameters using nonlinear least-squares optimization. The objective function to be minimized was the sum of the squared difference between measured data and model predictions within each trial, summed across all trials for each subject within each experiment. The optimization procedure minimized the objective function using the Levenberg–Marquardt algorithm (Moré, 1978), implemented with MATLAB's `lsqcurvefit` function (MATLAB, MathWorks, Natick, MA, USA). To avoid convergence problems associated with parameter optimization in time-delayed dynamical systems, we visually estimated each trial's time delay rather than treating it as a parameter to be optimized (Ferretti et al., 1996; Müller et al., 2003).

We assessed the goodness-of-fit of the estimated best-fit parameters using R^2 values to determine how much of the measured variance was explained by the model, and by examining the residuals between the model prediction and the measured data. We used paired *t*-tests to test for statistical differences in the timing and magnitude of the fast and slow process between the two experiments and present the summary statistics for these quantities using means and s.d. Because the assumption of normality was violated for the time delays (the time delays were close to 0 but positive by definition, resulting in a positive skew), we used the non-parametric Wilcoxon signed-rank test to test for statistical differences in time delays between the two experiments and present the summary statistics for time delays using medians and interquartile ranges. Finally, we used chi-square tests to determine whether the dynamics of the initial response depended upon the perturbation magnitude or direction. For all tests we considered $P < 0.05$ as significant.

Competing interests

The authors declare no competing financial interests.

Author contributions

All authors developed the concepts and approaches underlying this research. R.P. and M.S. performed the experiments and data analysis, with guidance and supervision by J.M.D. All authors prepared and edited the manuscript prior to submission.

Funding

This work was supported, in part, by US Army Research Office grant [W911NF-13-1-0268]; as well as Canadian Institutes of Health Research; and Michael Smith Foundation for Health Research salary awards, to J.M.D.

References

- Bertram, J. E. (2005). Constrained optimization in human walking: cost minimization and gait plasticity. *J. Exp. Biol.* **208**, 979-991.
- Bertram, J. E. and Ruina, A. (2001). Multiple walking speed-frequency relations are predicted by constrained optimization. *J. Theor. Biol.* **209**, 445-453.
- Cavagna, G. A., Thys, H. and Zamboni, A. (1976). The sources of external work in level walking and running. *J. Physiol.* **262**, 639-657.
- Coote, J. H., Hilton, S. M. and Perez-Gonzalez, J. F. (1971). The reflex nature of the pressor response to muscular exercise. *J. Physiol.* **215**, 789-804.
- Dietz, V., Quintern, J. and Sillem, M. (1987). Stumbling reactions in man: significance of proprioceptive and pre-programmed mechanisms. *J. Physiol.* **386**, 149-163.
- Donelan, J. M., Kram, R. and Kuo, A. D. (2001). Mechanical and metabolic determinants of the preferred step width in human walking. *Proc. R. Soc. B* **268**, 1985-1992.
- Donelan, J. M., Kram, R. and Kuo, A. D. (2002). Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking. *J. Exp. Biol.* **205**, 3717-3727.
- Eftman, H. (1966). Biomechanics of muscle with particular application to studies of gait. *J. Bone Joint Surg. Am.* **48**, 363-377.
- Ferretti, G., Maffezzoni, C. and Scattolini, R. (1996). On the identifiability of the time delay with least-squares methods. *Automatica* **32**, 449-453.
- Hayes, S. G., McCord, J. L., Koba, S. and Kaufman, M. P. (2009). Gadolinium inhibits group III but not group IV muscle afferent responses to dynamic exercise. *J. Physiol.* **587**, 873-882.
- IAAF (2008). *IAAF Track and Field Facilities Manual 2008*. Monaco: IAAF.
- Kaufman, M. P. and Hayes, S. G. (2002). The exercise pressor reflex. *Clin. Auton. Res.* **12**, 429-439.
- Kaufman, M. P., Longhurst, J. C., Rybicki, K. J., Wallach, J. H. and Mitchell, J. H. (1983). Effects of static muscular contraction on impulse activity of groups III and IV afferents in cats. *J. Appl. Physiol.* **55**, 105-112.
- McCloskey, D. I. and Mitchell, J. H. (1972). Reflex cardiovascular and respiratory responses originating in exercising muscle. *J. Physiol.* **224**, 173-186.
- Minetti, A. E., Capelli, C., Zamparo, P., di Prampero, P. E. and Saibene, F. (1995). Effects of stride frequency on mechanical power and energy expenditure of walking. *Med. Sci. Sports Exerc.* **27**, 1194-1202.
- Moré, J. (1978). The Levenberg-Marquardt algorithm: implementation and theory. *Numerical Analysis* **630**, 105-116.
- Müller, T., Lauk, M., Reinhard, M., Hetzel, A., Lücking, C. H. and Timmer, J. (2003). Estimation of delay times in biological systems. *Ann. Biomed. Eng.* **31**, 1423-1439.
- O'Connor, S. M. and Donelan, J. M. (2012). Fast visual prediction and slow optimization of preferred walking speed. *J. Neurophysiol.* **107**, 2549-2559.
- Orendurff, M. S., Schoen, J. A., Bernatz, G. C., Segal, A. D. and Klute, G. K. (2008). How humans walk: bout duration, steps per bout, and rest duration. *J. Rehabil. Res. Dev.* **45**, 1077-1089.
- Ralston, H. J. (1958). Energy-speed relation and optimal speed during level walking. *Int. Z. Angew. Physiol.* **17**, 277-283.
- Reynolds, R. F. and Bronstein, A. M. (2003). The broken escalator phenomenon. *Exp. Brain Res.* **151**, 301-308.
- Snaterse, M., Ton, R., Kuo, A. D. and Donelan, J. M. (2011). Distinct fast and slow processes contribute to the selection of preferred step frequency during human walking. *J. Appl. Physiol.* **110**, 1682-1690.
- Snyder, K. L., Snaterse, M. and Donelan, J. M. (2012). Running perturbations reveal general strategies for step frequency selection. *J. Appl. Physiol.* **112**, 1239-1247.
- Umberger, B. R. and Martin, P. E. (2007). Mechanical power and efficiency of level walking with different stride rates. *J. Exp. Biol.* **210**, 3255-3265.
- Verkerke, G. J., Hof, A. L., Zijlstra, W., Ament, W. and Rakhorst, G. (2005). Determining the centre of pressure during walking and running using an instrumented treadmill. *J. Biomech.* **38**, 1881-1885.