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Running perturbations reveal general strategies for step frequency selection

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Abstract

Recent research has suggested that energy minimization in human walking involves both a fast pre-programmed process and a slow optimization process. Here, we studied human running to test whether these two processes represent control mechanisms specific to walking or a more general strategy for minimizing energetic cost in human locomotion. To accomplish this, we used free response experiments to enforce step frequency with a metronome at values above and below preferred step frequency and then determined the response times for the return to preferred steady state step frequency when the auditory constraint was suddenly removed. In forced response experiments, we applied rapid changes in treadmill speed and examined response times for the processes involved in the consequent adjustments to step frequency. We then compared the dynamics of step frequency adjustments resulting from the two different perturbations to each other and to previous results found in walking. Despite the distinct perturbations applied in the two experiments, both responses were dominated by a fast process with a response time of 1.47 ± 0.05 s with fine-tuning provided by a slow process with a response time of 34.33 ± 0.50 s. The dynamics of the processes underlying step frequency adjustments in running match those found previously in walking, both in magnitude and relative importance. Our results suggest that the underlying mechanisms are fundamental strategies for minimizing energetic cost in human locomotion.

Key words: locomotion, energetics, neural control, step frequency

Introduction

A fundamental principle underlying locomotion physiology is that people select gait patterns that minimize energetic cost (1). For a given speed of locomotion, humans and other animals choose the gait that minimizes metabolic energy expenditure (18, 26). And within both walking and running gaits, people choose the step frequency that minimizes their energy use (9, 14-17, 20, 27, 33, 34). More generally, while people can certainly walk or run in many different ways, people consistently choose the patterns that minimize energetic cost.

Recent research on walking has suggested that there are at least two distinct processes that underlie the selection of energetically optimal gaits. Snaterse et al. (29) perturbed walking subjects with rapid changes in treadmill speed and measured the time scales involved in the subsequent adjustments to step frequency. They found that a component of their subjects' responses involved a gradual fine-tuning of step frequency towards the steady-state value. The timing of this slow process is consistent with direct optimization of energetic cost, which is expected to be slow for at least three reasons. First, candidate direct sensors of metabolic cost, such as chemoreceptors located in the medulla oblongata and the carotid and aortic bodies, as well as Group III and IV muscle afferents, are reported to require at least 5 seconds to produce physiological responses to a stimulus (21, 22). Second, instantaneous measures of energetic cost are not representative of the steady-state average, which is best assessed by integrating over at least one stride. Finally, the energy expenditure sensed at one particular step frequency does not indicate which other frequency will ultimately be optimal. It may be necessary for the person to iteratively adjust their step frequency, in a process that only gradually converges to the optimum.

The compounded effects of delays, averaging, and iterative convergence result in a slow direct optimization process that may take on the order of ten's of seconds to reach steady state.

While this slow process appeared to be important, the authors found that most of the step frequency adjustments were governed by a fast process that occurred within the first few seconds of a change in treadmill speed (29). Importantly, the speed of the adjustments was too rapid to be due to direct optimization of energetic cost. A second set of experiments demonstrated that this fast process encoded the relationship between speed and step frequency that minimized energetic cost. Consequently, the authors concluded that the fast process is a pre-programmed response—people rapidly predict the energetically optimal walking pattern based on prior knowledge of the relationship between their gait and metabolic cost.

The purpose of this paper is to test whether these fast and slow processes are specific to walking, or whether they represent general mechanisms underlying step frequency selection in human locomotion. To accomplish this, we tested for their presence in human running. This is a strong test of generality because our current understanding is that the biomechanics of the two gaits are quite different. Whereas walking is viewed as an inverted pendulum system with its motion governed by gravitational and inertial forces, running is viewed as a spring-mass system with stored elastic energy contributing to its motion (7). These biomechanical systems have different dynamic responses to perturbations (24, 25). Thus, finding similar dynamics of step frequency adjustments in running to those previously found in walking could not be explained by a simple mechanical response to perturbation. Instead, it would suggest that the same control strategies underlie gait parameter selection in walking and running, perhaps with the shared goal of minimizing energetic cost, as this is one characteristic common to both gaits (2, 7, 9, 11, 14, 15, 20).

We treat the person as a dynamic system that selects energetically optimal gaits using internal processes that can be identified by providing controlled inputs to the system and measuring its dynamic response (Figure 1A). Specifically, we performed a variety of different perturbations on running subjects and analyzed the time scales of the processes involved in their adjustments to step frequency. We focused on measuring step frequency because the preferred steady-state value minimizes metabolic cost, and there is a well-established energetic penalty for frequencies faster or slower than the preferred value (9, 14, 15, 20). To induce changes in step frequency, we used two different types of experimental perturbations, one involving physical changes and one in which the only environmental changes were sensory. In the forced response experiments, we applied rapid changes in treadmill speed to running subjects in a manner similar to Snaterse et al. (29), but additionally varied both size and direction of these changes. Though suggestive, these physical perturbations do not rule out a purely biomechanical response, so we also performed non-physical free response experiments. In the free response experiments, a metronome initially enforced step frequency at a value different than the preferred value, and we observed how step frequency changed once the metronome beat was replaced with white noise. To test whether the processes identified were specific to perturbation type and/or gait or instead represent general control mechanisms for selecting energetically optimal gait patterns during human locomotion, we compared the dynamics found in our different running perturbations to each other and to previous results for physical walking perturbations.

Materials and Methods

Subjects and Equipment

Eleven subjects participated in this study. All subjects (6 female, 5 male; body mass 62.6 ± 9.2 kg; leg length 0.93 ± 0.05 m; mean ± sd) were recreational athletes or members of the university track and field team. Simon Fraser University's Office of Research Ethics approved the protocol and all subjects gave written informed consent before participation.

Subjects ran on a treadmill (Trackmaster 425, Full Vision, Inc, USA) modified to allow the treadmill belt speed to be controlled by an analog input signal. The desired speed was dictated via computer in real time using a custom written program (Simulink Real-Time Workshop, Mathworks, Inc., Natick, MA). The actual speed was sampled at 1000 Hz using a magnet affixed to the treadmill flywheel and a reed sensor affixed to the treadmill chassis. We calculated step frequency from the time between consecutive foot-strikes determined using pressure sensitive transducers sampled at 500 Hz fixed to the soles of subjects' feet (Multimode Footswitches, Noraxon, Scottsdale, AZ). All data input and output was done via an analog/digital converter (National Instruments, Austin, TX) and saved for later analysis. We calculated step period from consecutive heel strikes, and a moving average of two consecutive steps was to nullify any differences in placement or sensitivity of the footswitches. Before any data were collected, we acclimated subjects using a 10-minute warm-up consisting of running on the treadmill at 2 m/s. Subjects were then asked to run briefly at the fastest and slowest speeds required by our protocol to verify that they could sustain the full range of speeds.

Free Response Experiments

During these experiments, subjects began running at a constant step frequency enforced using the beat of a metronome. After a period of time, the metronome beat was replaced by white noise (Figure 2A). Because the treadmill speed was fixed, subjects were required to keep their average speed constant once the frequency was released. However, subjects were not required to change their step frequency and any change could occur over any time scale. We examined whether subjects adjusted step frequency when the enforced frequency was released, and identified the time scales of the processes that contributed to any measured change.

Subjects ran at 3 m/s with step frequency first enforced by a metronome through headphones. We enforced four different step frequencies on each subject (Table 1). Two of these step frequencies were slower than the preferred value at 3 m/s with the first equal to the preferred step frequency at 2 m/s and the second defined as twice as slow. For instance, if a subject had a preferred step frequency of 2.8 Hz at 3 m/s and 2.5 Hz at 2 m/s, their slowest enforced frequency would be 2.2 Hz. The other step frequencies were faster than the preferred value with one equal to the preferred step frequency at 4.5 m/s and the other defined as twice as fast. Each trial was 100 seconds in duration and each condition was repeated three times for a total of 12 trials. The time at which the metronome beat was replaced with white noise was randomly assigned to be 30, 40, or 45 seconds. If a subject was unable to match the enforced step frequency by the last 10 seconds of step frequency restriction, the trial was not included in further analysis. This occurred in only 2 trials. One subject was found not to vary step frequency between 2 m/s and 3 m/s—we removed him from further analysis.

Forced Response Experiments

For these experiments, we suddenly changed treadmill speed and examined its effect on step frequency (Figure 2B). While this perturbation required subjects to immediately change speed in order to remain on the treadmill, they could change speed through any combination of step length and step frequency adjustments, including changing only step length while keeping step frequency constant. Importantly, the physical requirement of rapidly changing speed to remain on the treadmill does not specify any slow adjustments to step frequency. We compared the response times of the processes involved in step frequency adjustments in these forced response experiments with those identified in our free response experiments, with similar results indicating that common control mechanisms underlie the response to these distinct perturbations.

We imposed a series of step-like speed changes on subjects while they ran on the treadmill. They began running for 90 seconds at 2.0 m/s and then were given 90 second periods of speeds of 2.5, 3.0, 3.5, 4.0, and 4.5 m/s in random order, each with a recovery period of 90 seconds at 2.0 m/s between the intervals. The preferred step frequency was calculated to be the average step frequency from seconds 60-90. The maximum belt acceleration was set to 0.8 m/s^2 for both increases and decreases in speed. Depending on the magnitude of these perturbations, speed changes lasted for 0.8 to 5 seconds.

System Identification

We used standard techniques from system identification to quantify the dynamics of step frequency adjustments. System identification is a general term to describe algorithms for constructing mathematical models of dynamic systems from measured input-output data (23).

Based on previous research that had identified both a fast process and a slow process underlying the response to perturbations in walking (29), we used a two process model for parameter identification (Figure 1B). The mathematical representation of this model, expressed in the complex frequency domain, takes the form:

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

where *X(s)* is the input and *Y(s)* is the output (Figure 1C). The parameters τ_f and A_f represent the time constant and amplitude for the fast process. Correspondingly, the parameters τ_s and A_s represent the slow process time constant and amplitude. The parameter T_d is a time delay to account for fixed physiological time delays such as human reaction time. If the system input is an instantaneous step function of unit magnitude, and the system output is step frequency, *f*, the equivalent time domain expression is:

$$\Delta f(t) = A_f \left(1 - e^{\frac{-(t-T_d)}{\tau_f}}\right) + A_s \left(1 - e^{\frac{-(t-T_d)}{\tau_s}}\right), \tag{2}$$

where *t* is time and the remaining parameters are as defined above. Figure 1D illustrates how the output of this system in response to a step input is the sum of two exponential functions. The total response depends on the speed of the fast and slow processes as well as their relative contributions.

We used our measurements from the free response experiments to identify the unknown parameters in this two process model. To prepare the data for this analysis, we normalized each trial's change in step frequency from 0 to 1 by subtracting the initial step frequency and dividing the result by the difference between the ending and initial step frequencies. For instance, if the initial enforced step frequency was 3.0 Hz, and the ending step frequency was 2.8 Hz, these would convert to (3.0-3.0)/-0.2=0 and (2.8-3.0)/-0.2=1, respectively.

Preliminary analyses showed that some responses demonstrated an initial *undershoot* with the initial response approaching but not reaching the steady-state frequency (Figure 1D). Other trials demonstrated an initial *overshoot*, with the initial response overshooting the steady-state frequency (Figure 1D). Here, we define steady-state frequency as the average step frequency over the last 20 seconds of each trial. Before further analysis, we split the data from the free response experiments into two groups based on their initial response to the perturbation. We used the first group, the undershoot data, to identify the unknown parameters corresponding to the dynamics of the two mechanisms. Because the metronome was switched from a condition of being on to being off, we used a step function as the input for these free response experiments.

To calculate these best-fit parameters, we employed a gradient-descent based algorithm, seeded with an initial estimate of the parameter values. The identified parameters minimized the sum of the squared error between the model prediction and the measured step frequency adjustments for all undershoot trials. The identified parameters were insensitive to the initial estimates of parameter values. To implement this system identification, we used MATLAB's idproc.m and pem.m functions. We quantified the fast and slow processes using response time, defined to be the time required to achieve 95% of the total change for the given process (~3 times the time constant). We quantified the relative contributions of the two processes using the magnitudes of the amplitude parameters.

To test whether the measured adjustments to step frequency could be described by a simpler model, or if the dynamics were more complex than could be captured by our two process model, we also tested both one process and three process models. The degree to which the different models captured the measured responses was quantified by calculating R^2 values and by examining the residuals, defined as the difference over time between the model prediction and the measured data. We calculated R^2 values in two ways. The first calculation used the total error between the model prediction and the measured data for the individual trials by all subjects (individual fit). This is a very strict test—in the two process model, only five free parameters were used to describe the 43,086 total measurements from the free response undershoot data (10 subjects contributed 86 trials with each trial containing 501 data points). These comparisons led to deceivingly low R^2 values because the steady-state variability in step frequency was large relative to the step frequency changes induced by the perturbations. To reduce the effect of the steady-state variability on our goodness-of-fit metric, we also calculated the error between the model prediction and the average response across trials and subjects (average fit). This is still a strict test; the two process model used five free parameters to describe 501 data points equating to 496 statistical degrees of freedom.

System Validation

To test whether the identified processes were used consistently across all free response trials, we determined how well the two process model predictions fit the measured overshoot data. We fixed the time constants and the time delay identified from the undershoot data and did not allow these parameters to vary while we searched for the best-fit amplitude parameters. We did not fix the two amplitudes because we had no a priori prediction concerning the relative contribution of the two processes. We assessed model fit by calculating the residuals and the R^2 values for both the individual and average data.

We also tested whether the processes identified from the free response trials explained the measured responses to rapid changes in treadmill speed. We first eliminated any forced response trial that had a step frequency change of smaller than 0.03 Hz, a value within the noise of the step frequency measurement. Because subjects' step frequencies do not always change very much at slow speeds, this did occasionally occur, but only in 3 trials. Both the measured change in treadmill speed and the measured change in step frequency were then normalized to 1 for all trials as described earlier. Next, we binned the remaining data according to whether the initial response undershot or overshot the steady-state value. We then determined how well the two process model, identified from the free response undershoot trials, predicted the measured step frequency adjustments in response to this distinct perturbation. We fixed the time constants and the time delay parameters that were identified from the free response undershoot data, and searched for the best-fit amplitude parameters. The normalized treadmill speed was the input into this system identification. As with the earlier comparisons, we assessed model fit by calculating the residuals and the R^2 values for both the individual and the average data.

We used Chi-square tests to determine whether specific subjects, specific perturbation directions or specific perturbation magnitudes were more likely to exhibit undershooting or overshooting patterns. A p-value of 0.05 was considered significant.

Results

Free Response Experiments

When step frequency was enforced and then released, subjects exhibited rapid changes in step frequency followed by longer-term adjustments that gradually brought step frequency to its steady-state value. We used the undershoot data—where the initial adjustments in step frequency initially undershot the steady-state value—to identify the system dynamics and found that the measured dynamics were well described by a two process model (Equations 1 & 2; Figure 3A). The identified response times associated with each process differed by more than an order of magnitude, with values of 1.47 ± 0.05 seconds (mean ± standard deviation) for the fast process and 34.33 ± 0.50 seconds for the slow process. The fast process dominated the total response—the identified fast and slow process amplitudes were 0.67 ± 0.03 and 0.33 ± 0.03, respectively. The response to the perturbation began after a short delay (T_d=0.37 ± 0.02 seconds). The R^2 value for the average fit was 0.97, indicating that the model explained 97% of the average subject behavior. The R^2 value was lower for the individual fit, 0.36, because steady-state variability in step frequency was large relative to the step frequency changes induced by the perturbations. The residual errors also indicated that the two process model was a good fit—the errors were small in magnitude, randomly distributed around zero, and showed no particular pattern with time (Figure 3B).

Comparing the two process model fits with those from alternative models indicated that the simpler model was too simple, and a more complicated model was not needed to explain the measured results. A one process model was not sufficient to account for the observed adjustments in step frequency, leading to large residual errors that showed a distinct pattern over time (Figure 3B). This was also reflected in the R^2 values for the two process and one process model fits, which decreased from 0.36 to 0.25 for the individual fits and 0.97 and 0.80 for the average fits. The more complicated three process model did not provide any additional information when compared to our two process model—the R^2 values remained constant for the individual and average fits, respectively. Taken together, these comparisons suggest that a two process model is the simplest model required to describe the measured dynamics.

The two process model also accurately described the step frequency adjustments that initially overshot the steady-state value, indicating that the identified processes were used consistently across all free response trials (Figure 3C and 3D). This is evident from the small changes in R^2 values which decreased only slightly to 0.95 from 0.97 for the average fit comparisons and increased to 0.54 from 0.36 for the individual fit comparisons. The goodness of fit was also evident from the low magnitudes, random distribution, and lack of pattern observed in the residual errors (Figure 3D). The quality of this fit was particularly impressive given that the time constants and time delay parameters were fixed at the values identified from the undershoot data leaving only the two amplitude parameters to vary when fitting the overshoot data. For this overshoot data, the fast and slow process amplitudes were 1.33 ± 0.01 and -0.33 ± 0.01, respectively. Thus, in both undershoot and overshoot free response data, the fast process brought the step frequency within 33% of the steady-state value while the slow process fine-tuned the result.

Forced Response Experiments

Subjects exhibited similar behavior in the forced response experiments as in the free response experiments—there was a fast response followed by a longer-term adjustment of step frequency to its final value (Figure 4). We made model predictions for the forced response experiments by keeping the time constants and time delay parameters fixed at the values identified from the free response undershoot data, leaving only the two amplitude parameters to vary. The time constants and delay identified from the free response data were a good fit to the data measured in this distinct experimental perturbation with average fit R^2 values of 0.67 and 0.87 and individual fit R^2 values of 0.19 and 0.38 for the undershoot and overshoot data, respectively. The identified amplitudes were similar between the two experiments, with undershoot amplitudes of 0.78 ± 0.01 and 0.23 ± 0.01 and overshoot amplitudes of 1.40 ± 0.01 and 0.40 ± 0.01 for the fast and slow processes, respectively.

The two process model identified from the free response experiments did not entirely explain the adjustments in step frequency in response to the perturbation to treadmill speed—there were some additional dynamics that occurred within the first few seconds (Figure 4B and 4D). This difference was not unexpected—while the metronome provided an impulsive auditory perturbation, the treadmill provided a physical perturbation that was stretched out over a finite period of time. The additional measured dynamics took place during the speed changes, and the residual errors paralleled the acceleration of the treadmill, indicating that they may simply reflect a biomechanical response to the treadmill acceleration (Figure 4B and 4D). These additional dynamics did not replace those resulting from the fast and slow processes, but supplemented them.

Walking and Running Compared

The processes that we identified in running match those found previously in walking, suggesting that common mechanisms underlie step frequency selection across gaits. Snaterse et al. (29) perturbed walking subjects by changing treadmill speed and identified a fast process response time value of 1.4 ± 1.1 seconds, albeit with different mathematical methods, which is very similar to running's fast process response time of 1.5 ± 0.1 seconds. A similar correspondence is observed for the slow process response times (27.6 ± 16.2 seconds for walking and 34.3 ± 0.3 seconds for running). In addition, the relative contributions of the fast and slow processes were similar between walking and running. The fast process adjusted step frequency to within 34% of the final steady-state value during walking, and to within 23-40% of the final value during running, depending on the type of perturbation.

Discussion

Our results indicate that distinct fast and slow processes contribute to step frequency selection during human locomotion. The fast process dominates the overall response to perturbations, rapidly completing two thirds of the total step frequency change. The slow process takes about 20 times longer to fine tune step frequency and complete the return to the energetically optimal gait. This is a robust finding; we identified the same two processes in both walking and running irrespective of whether subjects overshot or undershot the steady-state value and irrespective of whether the experiment physically perturbed the subjects or simply released them from an auditory constraint. We also found that the relative contributions of the fast and slow processes were similar between walking and running, suggesting that not only do common mechanisms underlie step frequency selection, but that the mechanisms are of comparable importance across gaits. This consistency may reflect a similar uncertainty in the frequency prediction of the fast pre-programmed response, with the body trying to maximize the benefit of the speed of this process while minimizing the cost of its inaccuracy. Finding similar dynamic responses to perturbations in both walking and running, despite very different biomechanical mechanisms underlying the two gaits (7), suggests that the two gaits share some of the same underlying control strategies. The most likely control goal is metabolic cost minimization as preferred steady-state step frequency minimizes metabolic cost in both gaits (9, 14, 15, 20).

One difference between the walking and running results was the distinct bifurcation in initial response to running perturbations, with some responses initially undershooting the steady-state step frequency while others initially overshot. While there was variability in the amount of overshoot or undershoot, these were clear categories, not arbitrary groupings of continuously varying responses. To further understand this pattern, we determined whether it was dependent on individual subjects or conditions. The only general pattern that emerged was that subjects were more likely to undershoot than to overshoot in both experiments ($p=2.0 \times 10^{-8}$, Chi-square test). In the free response and forced response experiments, 73% and 65% of the trials were undershoots, respectively. There were some additional experiment-specific effects. In the free response experiments, the direction of perturbation had a significant effect on the initial response with subjects more likely to overshoot when released from a frequency higher than preferred ($p=8.8 \times 10^{-6}$). In the forced response experiments, some subjects were more likely to overshoot than undershoot ($p=0.03$). However, we did not find a direction-specific effect in the forced response experiments, or a subject-specific effect in the free response experiments, and neither experiment demonstrated a statistically significant effect of perturbation magnitude on the initial response. While it is not clear why some subjects in some conditions initially overshot the steady-state value, the combination of short and long term processes still captured the observed dynamics very well.

There were a number of important limitations to our study. First, treadmills impose a speed constraint that does not exist when moving overground. We have performed free response pilot experiments on subjects overground (unpublished), and the preliminary results suggest that our observations are not specific to treadmill locomotion. A second limitation is that we draw conclusions about energy minimization without directly measuring metabolic cost. This reflects a conscious decision to focus on collecting a wide range of perturbations, which eliminated the possibility of having the long duration trials that are required to accurately determine 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 minimizes metabolic cost (9, 14, 15, 20). There are other running parameters that could be manipulated to change metabolic cost (e.g. step width), but none so readily as step frequency. For the current experimental protocol, our conclusions regarding step frequency apply equally to step length. This is because the treadmill always specified running speed and speed is the product of step frequency and step length.

Our current experiments do not allow us to definitively conclude which physiological pathways are responsible for the fast and slow processes. Spinal reflexes, central pattern generators, and descending commands from the brain may all play a role in both processes, and we cannot partition their contributions without further experiments. However, our current results do exclude some important possibilities. First, the processes are not simply biomechanical responses to a perturbation. This is most clear from the free response experiments where the perturbations were strictly auditory and all physical adjustments were self-induced. While there were physical perturbations in the forced response experiments, we observed additional fast adjustments to step frequency that occurred during the perturbations (Figure 4).

Second, the fast process we have identified is not the same phenomenon as the stumbling reaction reflex. Previous studies of the stumbling reaction reflex employed conceptually similar treadmill belt speed perturbations to our forced response experiments (4, 10). However, the belt accelerations used in these experiments were designed to challenge the balance of their walking subjects and were more than ten times greater than those in our experiment (11.2 m/s^2 vs. 0.8 m/s^2). Furthermore, our free response experiments clearly demonstrate fast adjustments to step frequency even though balance was not challenged with a physical perturbation.

Finally, the fast process is too rapid to involve direct optimization of metabolic energy expenditure. The fast adjustments were essentially complete in under two seconds whereas feedback from physiological sensors that sense signals directly related to metabolic activity is reported to require at least five seconds to initiate physiological responses to a metabolic stimulus (3, 13, 19, 21, 22). We consider this fast process pre-programmed because it contributes to producing the energetically optimal response without current knowledge of the actual energetic cost, relying instead on prior knowledge of the association between gait and metabolic cost. The name ‘pre-programmed’ is not meant to imply that this response involves no feedback whatsoever, as it may be triggered from vision, proprioception, or other sensory systems, and it may involve feedback mechanisms known to underlie the control of locomotion, including spinal reflexes (28). In contrast to the speed of the fast process, the approximately 30 second response time of the slow process is consistent with the expected timing of direct optimization of metabolic cost. As we described in the introduction, direct optimization is likely slowed by the compounded effects of feedback delays, averaging, and iterative convergence.

There are important energetic advantages to using both optimization and pre-programming in the control of step frequency. An advantage to optimization is accuracy—it can automatically adjust to novel circumstances, such as variable terrain or carrying a load, to converge on the energetically optimal gait. The magnitude of this energetic benefit will vary with the specifics of the situation as it depends on the precision of the pre-programming and how long the steady-state gait is maintained. The addition of a fast pre-programmed process also has a clear energetic advantage over using optimization alone in that it can better track the energetically optimal step frequency in response to continuously varying speeds. This advantage is largest for intermediate speed changes—optimization alone can track the optimal step frequency when speed is changing very slowly and neither process can adjust sufficiently fast when speed is changing very quickly.

To be more quantitative, we used our identified processes to compare how a continuously varying speed affected the metabolic cost of running when using both processes, or just the slow process, to track the optimal step frequency. Considering speeds that sinusoidally oscillated between 2 m/s and 6 m/s, the difference between these two situations in their ability to track the optimal step frequency was maximized with sinusoid periods of 18 seconds. At this period, running using the slow process alone required an approximately 5% greater metabolic cost when compared to using both processes to select step frequency. We estimated this penalty using the known relationship between a change in step frequency away from preferred and the consequent increase in metabolic cost (30). The percentage difference is relatively small because the relationship between speed and the energetically optimal step frequency is relatively flat in running—even for large speed changes, the old optimal step frequency is not far from the new optimal step frequency (8). However, the magnitude of this penalty is not trivial—a 5% increase in metabolic cost when running at 4 m/s equates to about a 40 Watt penalty for a 70 kg runner. Furthermore, if conditions require variability at relatively fast speeds, any metabolic penalty may push the runner over their lactate threshold, greatly reducing the duration of the run (12). Under the conditions in which running evolved, where humans may have often been involved in an extended chase (5, 6), using a fast pre-programmed process to maximize the sustainable running speed may have been an important determinant of survival.

These results relate directly to theories of optimal pacing strategy in running races. Researchers have suggested that athletes choose their initial pace based on previous experience and environmental conditions—analogous to the role of the pre-programmed process and then adjust their pace during the race based on feedback from physiological sensors—analogous to the direct optimization process (31, 32). Our results suggest that the role of pre-programming likely goes beyond estimating initial race pace because, as described in the previous paragraph, optimization is too slow to keep up with rapid changes to speed characteristic of race surges. Racers who develop very accurate pre-programmed processes would be at an advantage in these situations—they could quickly select the metabolically optimal gait for the changing speeds. It may even be a good strategy for these racers to inflict surges, and their consequent metabolic penalty, on the competitors with less accurate predictive mechanisms.

In summary, we found that two processes underlie the selection of the energetically optimal gait in human locomotion. Our subjects relied heavily on pre-programmed gaits to rapidly select their preferred step frequency, and then gradually fine-tuned that selection, perhaps using direct optimization. The addition of a fast pre-programmed process has a clear energetic advantage over using optimization alone in that it can better track the energetically optimal step frequency in response to continuously varying speeds. We observed these two processes irrespective of whether subjects overshot or undershot the steady-state value and irrespective of whether the experiment physically perturbed the subjects or simply released them from an auditory constraint. Furthermore, the processes seen in running match those found in walking, both in timing and relative importance, suggesting that the mechanisms underlying these two processes are universal strategies for minimizing energy in locomotion.

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Figure Legends

Figure 1. General Strategies Underlying the Selection of Step Frequency A) We treat the person as a dynamic system that selects energetically optimal gaits using internal processes that can be identified by providing controlled inputs to the system and measuring its dynamic response. B) Based on previously walking research, we hypothesized that a combination of a fast pre-programmed process and a slow direct optimization process underlie the selection of energetically optimal running gaits. C) Mathematically, these processes can be represented by two transfer functions that act on two different time scales. D) Illustrations of the possible system responses to a step input. If only the fast process is active, the system rapidly reaches steady-state and never overshoots the steady-state value (dotted line). If only the slow process is active, the system gradually approaches the steady-state value (dashed line). If both processes are active, the fast process can result in the system either initially undershooting or overshooting the steady state value (dot-dash lines). The slow process will cause the system to gradually converge to the steady-state value. Whether an overshoot or undershoot occurs is determined entirely by the relative contribution of the two processes, which is determined by their amplitudes and not by their time constants. The right-hand side of the grey box illustrates the onset of the step input.

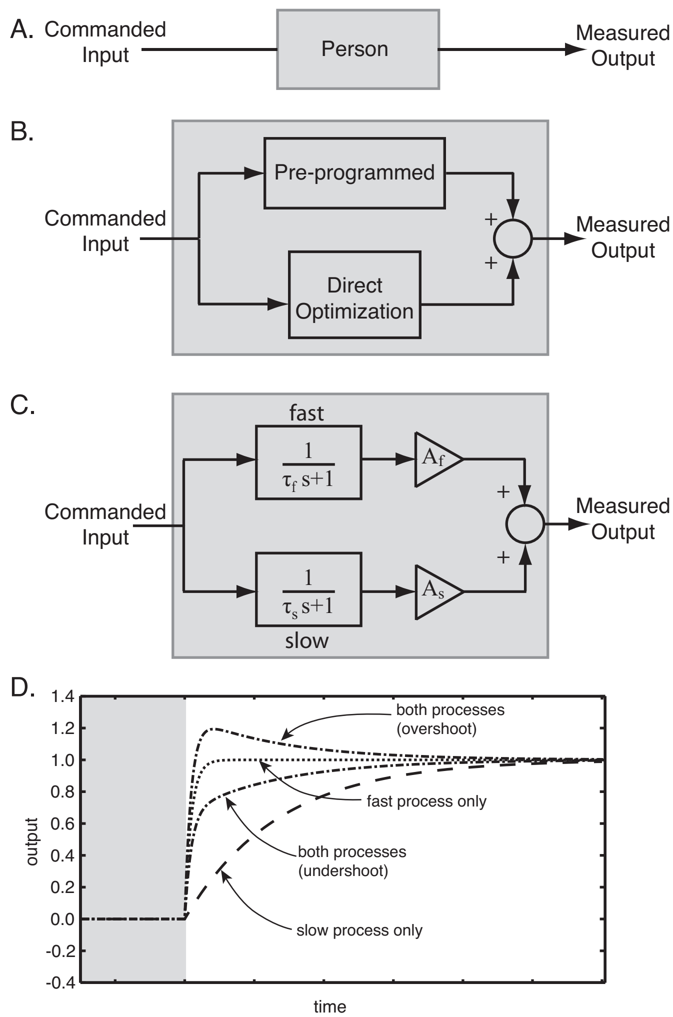
Figure 2. Experimental Methodology. A) In our free response experiment, subjects began running at a constant step frequency enforced using the beat of a metronome played through headphones. After a period of time, the metronome beat was replaced by white noise. Speed was kept fixed. B) In our forced response experiment, we suddenly changed treadmill speed. In both experiments, we measured any immediate and long-term adjustments to step frequency that occurred in response to the perturbations.

Figure 3. Free Response Results. When step frequency was enforced and then released, subjects exhibited rapid changes in frequency followed by longer-term adjustments that gradually brought frequency to its steady-state value. The top and bottom rows present the undershoot and overshoot data, respectively. A) 1 process (grey line) and 2 process (thick black line) models were fit to the undershoot experimental data using a step input (dotted line) to represent the change in the metronome signal. B) The residual error between the model and the experimental data shows that the 1 process model (grey line) was not sufficient to describe the dynamics. We also fit a 3 process model, but it was so similar to the 2 process model (black line) that it could not be shown without obscuring the residuals resulting from the 2 process fit. C) The time constants identified for the undershoot data were fixed and the amplitudes allowed to vary to find a 2 process fit (thick black line) for the overshoot data (black line), again using a step input (dotted line) to represent the metronome. D) The residual error shows that this fit also very closely matched the overshoot experimental data. In all graphs, the grey area is used to indicate the period prior to the onset of the perturbation (i.e. when the metronome was on). For clarity, we present the average data over all trials.

Figure 4. Forced Response Results. When speed was rapidly changed, subjects exhibited similar behavior to the free response experiments—there was a fast response followed by a longer-term adjustment of step frequency to its final value. The top and bottom rows present the undershoot and overshoot data, respectively. A) The 2 process fit using the time constants identified for the undershoot free response data (thick black line) also matched the forced response undershoot

data well with the normalized treadmill speed used as input (dotted line). B) The residual errors demonstrated that there were some additional dynamics (black line) involved in the forced response data that strongly paralleled the acceleration of the treadmill (grey line). C) The 2 process fit (thick black line) also closely approximated the overshoot forced response data. D) the residual errors for the overshoot data also demonstrated additional dynamics (black line) that corresponded to the treadmill acceleration (grey line). In all graphs, the grey area is used to indicate the period prior to the perturbation (i.e. when the treadmill was at its initial speed). For clarity, we present the average data over all trials.

Table 1.We enforced four step frequencies for each subject at 3 m/s. The intermediate slow step frequency was enforced to be the subject's preferred step frequency at 2 m/s. The slowest step frequency was twice as far from preferred step frequency at 3 m/s as the subject's preferred step frequency at 2 m/s. Similarly, the intermediate fast step frequency was enforced to be the subject's preferred step frequency at 4.5 m/s. The fastest step frequency was twice as far from preferred step frequency at 3 m/s as the subject's preferred step frequency at 4.5 m/s.


A.
Commanded Input
Person
Measured Output
B.
Commanded Input
Pre-programmed
Direct Optimization
+
+
Measured Output
C.
fast
$\frac{1}{\tau_f s+1}$
A_f
Commanded Input
$\frac{1}{\tau_s s+1}$
A_s
slow
+
+
Measured Output
D.
both processes (overshoot)
fast process only
both processes (undershoot)
slow process only
output
time
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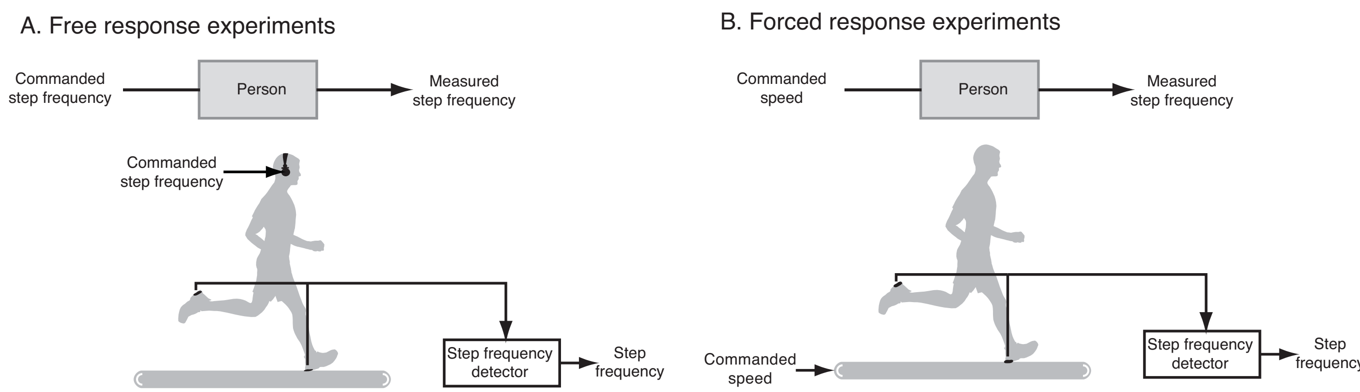
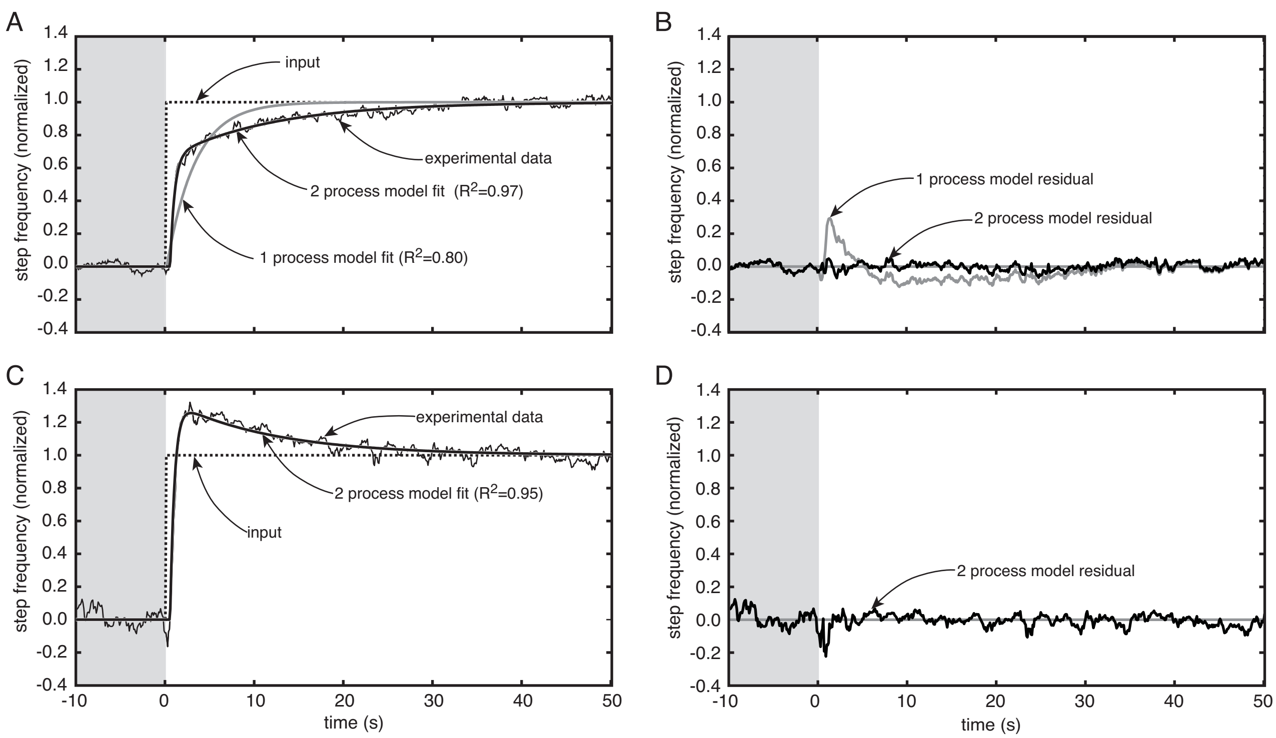
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4


A. Free response experiments
Commanded step frequency
Person
Measured step frequency
Commanded step frequency
Step frequency detector
Step frequency
B. Forced response experiments
Commanded speed
Person
Measured step frequency
Commanded speed
Step frequency detector
Step frequency


A
B
C
D
input
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1 process model fit (R2=0.80)
1 process model residual
2 process model residual
2 process model fit (R2=0.95)
step frequency (normalized)
time (s)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-10
0
10
20
30
40
50

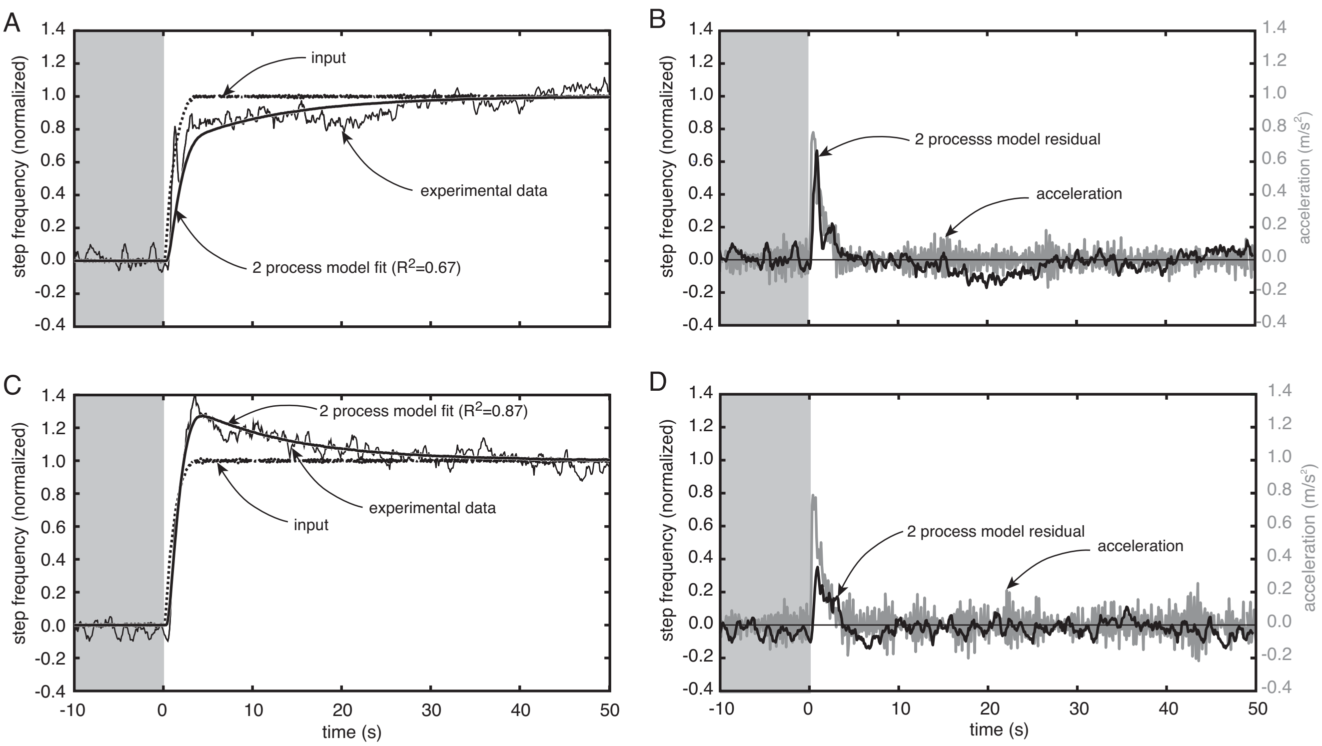
A
B
C
D
input
experimental data
2 process model fit (R2=0.67)
2 processs model residual
acceleration
2 process model fit (R2=0.87)
2 process model residual
step frequency (normalized)
acceleration (m/s2)
time (s)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-10
0
10
20
30
40
50

Table 1. Enforced and preferred step frequencies at 3 m/s for each subject.

Subject	Enforced Slowest Step Frequency (Hz)	Enforced Slower Step Frequency (Hz)	Preferred Stride Frequency at 3 m/s (Hz)	Enforced Faster Step Frequency (Hz)	Enforced Fastest Step Frequency (Hz)
1	2.40	2.57	2.75	3.17	3.59
2	2.40	2.52	2.65	2.90	3.16
3	2.55	2.71	2.86	3.08	3.30
4	2.44	2.68	2.92	3.28	3.64
5	2.48	2.65	2.81	3.09	3.37
6	2.39	2.54	2.68	2.91	3.14
7	2.52	2.67	2.81	3.06	3.32
8	2.40	2.51	2.73	2.99	3.25
9	2.74	2.84	2.95	3.14	3.33
10	2.59	2.69	2.79	3.02	3.25