Distinct fast and slow processes contribute to the selection of preferred step frequency during human walking

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[2]*Faculty of Human Movement Sciences, VU Univiversity, Amsterdam, The Netherlands; and* [3]*Department of Mechanical Engineering, University of Michigan, Ann Arbor, Michigan*

Snaterse M, Ton R, Kuo AD, Donelan JM. Distinct fast and slow processes contribute to the selection of preferred step frequency during human walking. *J Appl Physiol* 110: 1682–1690, 2011. First published March 10, 2011; doi:10.1152/japplphysiol.00536.2010.— Humans spontaneously select a step frequency that minimizes the energy expenditure of walking. This selection might be embedded within the neural circuits that generate gait so that the optimum is pre-programmed for a given walking speed. Or perhaps step frequency is directly optimized, based on sensed feedback of energy expenditure. Direct optimization is expected to be slow due to the compounded effect of delays and iteration, whereas a pre-programmed mechanism presumably allows for faster step frequency selection, albeit dependent on prior experience. To test for both pre-programmed selection and direct optimization, we applied perturbations to treadmill walking to elicit transient changes in step frequency. We found that human step frequency adjustments (*n* = 7) occurred with two components, the first dominating the response (66 ± 10% of total amplitude change; mean ± SD) and occurring quite quickly (1.44 ± 1.14 s to complete 95% of total change). The other component was of smaller amplitude (35 ± 10% of total change) and took tens of seconds (27.56 ± 16.18 s for 95% completion). The fast process appeared to be too fast for direct optimization and more indicative of a pre-programmed response. It also persisted even with unusual closed-loop perturbations that conflicted with prior experience and rendered the response energetically suboptimal. The slow process was more consistent with the timing expected for direct optimization. Our interpretation of these results is that humans may rely heavily on pre-programmed gaits to rapidly select their preferred step frequency and then gradually fine-tune that selection with direct optimization.

locomotion; energetics; neural control

HUMANS AND OTHER ANIMALS SELECT walking patterns that appear to minimize energetic cost. They tend to locomote at a speed near that which minimizes the metabolic energy cost per unit distance traveled (31). And at a given speed, the nervous system selects a combination of step frequency and step length that coincides with the minimum rate of metabolic energy expenditure (16, 17, 26, 37, 40). Although this principle was established over 50 years ago (31), the mechanisms underlying the selection of preferred gait patterns and their relation to metabolic cost minimization are not yet understood (33–35).

One possible mechanism for selecting the optimum is simply to recall a gait pattern pre-programmed or embedded within the neural circuitry that controls locomotion. For example, the energetically optimal gaits may be encoded within the feed-back gains of spinal reflexes or the timing circuits of central pattern generators (28). These pre-programmed gaits could be triggered by feedback from vision, proprioceptors, or other sensory receptors on sensing a perturbation away from the preferred gait. Although pre-programmed gaits can be selected rapidly, they suffer from an important drawback: the central nervous system (CNS) needs prior experience with specific gaits in specific situations to accurately select the energetically optimal pattern. But a variety of nonconstant biomechanical and environmental factors, such as footwear, carried load, or walking surface, affect energetic cost. Were the CNS to rely entirely on pre-programmed gaits, it would be unable to reliably produce the energetically optimal gait in all contexts.

An alternative mechanism that does not require prior experience is for the CNS to directly sense energetic cost and dynamically adapt the gait to minimize it. A number of physiological sensors may provide such direct sensing. For example, chemoreceptors in the medulla oblongata and the carotid and aortic bodies are sensitive to changes in blood oxygen and carbon dioxide concentrations associated with metabolic demand, and play an important role in the control of ventilation (4, 8, 12, 15, 27, 29, 32). More peripheral feedback, such as from group IV muscle afferents, may provide information about muscle metabolism or its by-products, as with the exercise pressor reflex that increases heart rate and ventilation on onset of exercise (1, 2, 13, 14, 18, 19). Feedback from central and peripheral receptors may be integrated by the CNS and used to minimize the sensed metabolic cost in an online direct optimization process.

A likely drawback of direct optimization is a relatively slow response time. The known direct sensors of metabolic cost produce relatively slow physiological responses, with the smallest reported delays of ~5 s (9, 14, 18, 20, 24). If similar feedback were used in the control of walking, convergence to an energetically optimal gait would be a gradual process. Convergence might also be slow simply because steady-state expenditure is best assessed over multiple steps. Even then, the energy expenditure sensed at one instance does not necessarily indicate what gait pattern will ultimately be optimal, potentially necessitating an iterative process. The compounded effect of delays, averaging, and iteration is to make the optimization process slow, likely occurring over tens of seconds or longer.

The goal of the present study was to gain insight into the mechanisms underlying the selection of preferred gait patterns by perturbing walking speed and measuring adjustments to step frequency. We specifically focused on step frequency, because preferred frequencies minimize metabolic cost at all steady-state walking speeds and there is a well established energetic

penalty for frequencies faster or slower than the preferred value (5, 6, 16, 17, 26, 37, 40). Although there is little to distinguish pre-programmed gaits from direct optimization during normal steady-state walking, they will differ in their transient response to perturbations. Consequently, we applied rapid changes to treadmill speed and measured the dynamics of step frequency adjustments. Observations of fast and slow dynamics in the adjustments would suggest contributions from pre-programming and direct optimization, respectively. We also applied perturbations designed to deceive a pre-programmed selection of step frequency by using novel contexts to experimentally alter the energetically optimal gait pattern. Slow convergence to the energetically optimal speed-frequency combination would suggest direct optimization, whereas rapid attraction to the normal but energetically suboptimal combination of speed and frequency would suggest a reliance on pre-programmed gaits.

METHODS

Seven naive adult volunteers (5 men, 2 women; body mass 69.6 ± 8.1 kg; leg length 0.92 ± 0.03 m; means ± SD) participated in these experiments designed to characterize the dynamics of step frequency adjustments using two types of perturbations to treadmill walking (Fig. 1, *A* and *B*). The experiments were performed over 2 days, with no more than 60 min of walking per day, to reduce fatigue effects. To habituate to treadmill walking, subjects began each day with at least 10 min of treadmill walking at different constant speeds (38, 39). Simon Fraser University's Office of Research Ethics approved the protocol, and participants gave their written, informed consent before experimentation.

Open-loop perturbations. The first type of perturbations applied sudden open-loop changes in treadmill speed. These were intended to elicit transient adjustments of step frequency toward the energetically optimal frequency for the new speed. Observing fast and slow dynamics in the adjustments would suggest a contribution from pre-programming and direct optimization, respectively. Although these
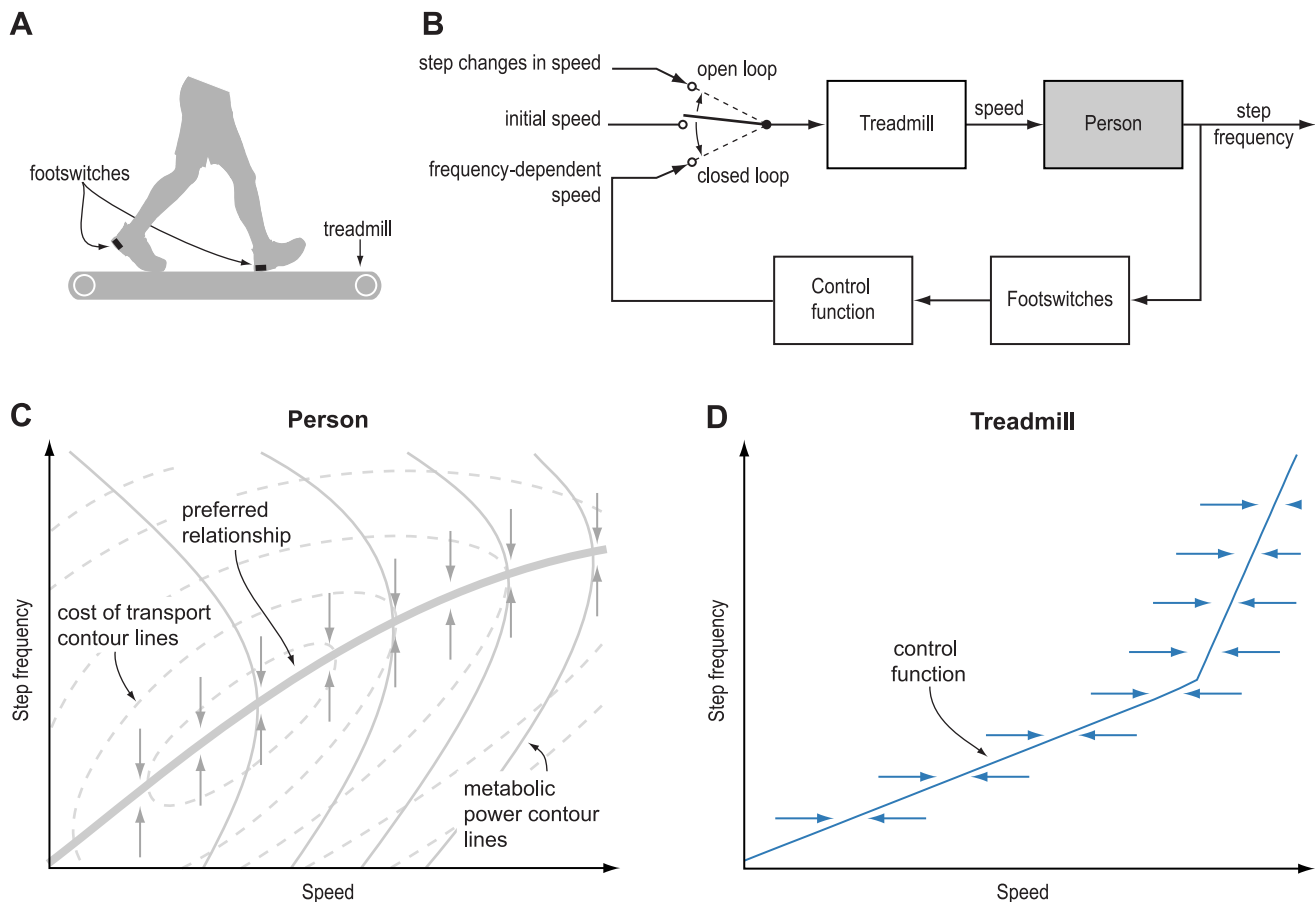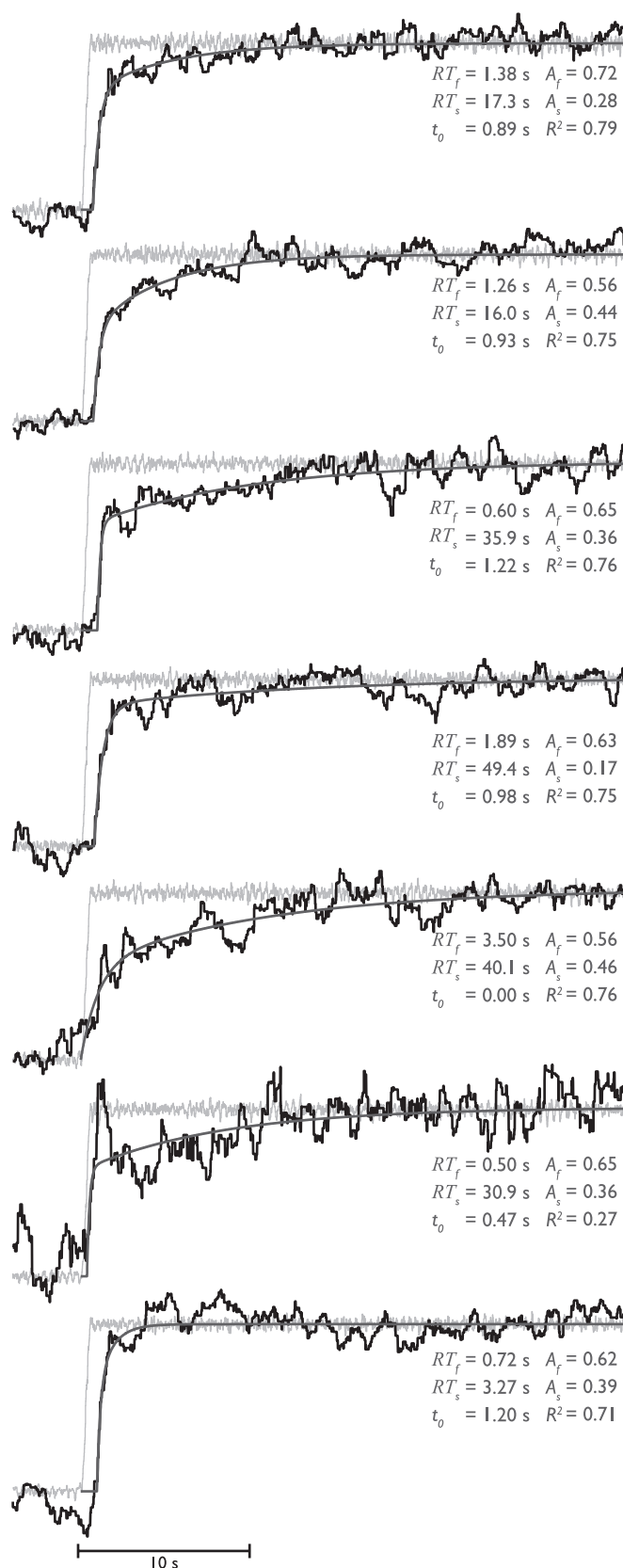

Fig. 1. Experimental setup. *A*: subjects walked on a treadmill that applied speed perturbations while we measured instantaneous step frequency using footswitches. *B*: two types of speed perturbations were applied, starting from a steady initial speed. Open-loop perturbations consisted of rapid changes in treadmill speed. Closed-loop perturbations used a feedback controller to make treadmill speed dependent on the subject's step frequency, based on a specified control function. *C*: as a function of walking speed, humans prefer the step frequency that minimizes metabolic cost, represented here by contours of both constant metabolic power [thin solid gray lines (3)] and constant cost of transport (thin dashed gray lines). We refer to this preference as the preferred relationship (thick gray line). When walking with a step frequency different from the preferred frequency, the person's tendency is to adjust their step frequency toward the preferred value at that speed (as illustrated by the vertical gray arrows). *D*: similarly, the treadmill adjusts its speed toward the control function value corresponding to the currently measured step frequency during closed-loop perturbations (as illustrated by the horizontal blue arrows).

RT_f = 1.38 s A_f = 0.72
RT_s = 17.3 s A_s = 0.28
t_0 = 0.89 s R^2 = 0.79

RT_f = 1.26 s A_f = 0.56
RT_s = 16.0 s A_s = 0.44
t_0 = 0.93 s R^2 = 0.75

RT_f = 0.60 s A_f = 0.65
RT_s = 35.9 s A_s = 0.36
t_0 = 1.22 s R^2 = 0.76

RT_f = 1.89 s A_f = 0.63
RT_s = 49.4 s A_s = 0.17
t_0 = 0.98 s R^2 = 0.75

RT_f = 3.50 s A_f = 0.56
RT_s = 40.1 s A_s = 0.46
t_0 = 0.00 s R^2 = 0.76

RT_f = 0.50 s A_f = 0.65
RT_s = 30.9 s A_s = 0.36
t_0 = 0.47 s R^2 = 0.27

RT_f = 0.72 s A_f = 0.62
RT_s = 3.27 s A_s = 0.39
t_0 = 1.20 s R^2 = 0.71

10 s

perturbations would require subjects to immediately adjust their walking speed to remain in position on the treadmill, they would also allow subjects considerable freedom in the time course of their step frequency response, so long as step length is also adjusted to yield the appropriate speed. For the remainder of this study, we refer only to speed and step frequency, with the understanding that step length may be found by dividing speed by step frequency.

The open-loop perturbations consisted of 10 sudden stepwise increments in treadmill speed. Increments occurred every 90 s in equally spaced steps between the lowest and highest speeds (0.35 m/s and 1.93 m/s, respectively). These different speed conditions were also used to determine the preferred speed-frequency relationship for each subject (Fig. 1*C*). Each subject's preferred speed-frequency relationship was determined by averaging step frequency over the last 30 s for each speed and then fitting a quadratic function to these steady-state frequencies (yielding R^2 values ranging from 0.96 to 0.99).

We used a two-process model to quantify the time course and relative contribution of fast and slow components to the open-loop response. This model was the sum of two exponentially decaying changes of the form

$$\Delta f(t) = A_f\left[1 - e^{-(t-t_0)/\tau_f}\right] + A_s\left[1 - e^{-(t-t_0)/\tau_s}\right] \qquad (1)$$

where Δf is change in step frequency, t is time, t_0 is a time delay, A_f and A_s are amplitudes of fast and slow changes, respectively, and τ_f and τ_s are the corresponding exponential time constants characterizing the rate of change. The exponential time constants were used to calculate the 95% response times, defined as the durations necessary for one component to complete 95% of its change (or about three exponential time constants). This model was fit to the average response for each subject, rather than individual trials, to reduce sensitivity to noisy measurements.

Closed-loop perturbations. The second type of perturbations used a closed-loop feedback controller to specify treadmill speed based on the subject's instantaneous step frequency. These closed-loop perturbations prescribe a steady-state relationship between speed and frequency through a control function (Fig. 1*D*) that differs from the normally preferred speed-frequency relationship (Fig. 1*C*). The purpose of the closed-loop perturbation was to create a situation in which direct optimization and pre-programming would produce different steady-state behaviors. If step frequency is mostly determined by direct optimization, subjects would be expected to slowly settle into the combination of speed and frequency along the control function that minimizes their metabolic cost irrespective of their normally preferred gait patterns. However, if subjects mainly employed selection of pre-programmed step frequencies for each speed they encountered, they would be expected to rapidly adjust their step frequency according to their normally preferred speed-frequency relationship (Fig. 1*C*) irrespective of the actual energetic minimum. In this latter situation, the gait might transiently deviate from both the control function and the preferred relationship, but a steady state in speed and frequency could only occur at an intersection of the control function and preferred relationship, because only then would the requirements

Fig. 2. Responses to open-loop perturbations. The averaged step frequency response (black line) to 10 rapid changes in treadmill speed (light gray line) is shown for each subject. The dark gray line illustrates the two-process model (*Eq. 1*) that best fits each subject's response. Model parameters and R^2 values for each fit are presented on the right-hand side of each panel (RT_f and RT_s, 95% response time of fast and slow changes; A_f and A_s, corresponding amplitudes; t_0, time delay). Before we averaged the data, we normalized all frequency and speed changes to unity by subtracting the steady-state values before the speed change and dividing by the amplitude of change. The 95% response time, defined as the duration necessary for one component to complete 95% of its change, was determined from the exponential time constants found by fitting *Eq. 1*.

of the treadmill controller and the pre-programmed preferred relationship both be satisfied.

Each control function trial consisted of an initial 90-s-long open-loop interval followed by another 90-s interval in which the control function was engaged. In the open-loop interval, subjects walked at their preferred frequency for a prescribed constant speed, thereby setting an initial condition. Starting from this initial condition, the closed-loop control function adjusted treadmill speed according to the person's step frequency. Although an initial adjustment in treadmill speed would require subjects to immediately adjust their own speed to remain on the treadmill, they would otherwise be free to select their step frequency and the time course of their response, as long as their speed remained at or near that specified by the control function. Subjects experienced each control function twice, with a randomized order of initial conditions. We used the final third of each 90 s interval to determine each subject's steady-state behavior.

To compare the steady-state behavior with the energetically optimal response, we measured energy expenditure at six predetermined speed-frequency combinations along the control function. Subjects were asked to walk to the beat of a metronome, with the closed-loop control function engaged, to yield the desired steady-state step frequency and speed. To test whether the dynamics of the control function influenced these results, we also determined metabolic cost at three of the above speed-frequency combinations (1.37, 1.83, 2.06 Hz) with the speed held constant. We found no significant difference due to closed-loop control ($P = 0.54$). Walking trials were conducted in random order. We determined metabolic cost by measuring rates of oxygen consumption and carbon dioxide production using indirect calorimetry (Vmax Encore 29s, SensorMedics). Each of these trials included an initial 3 min for subjects to reach steady state (30), followed by 2 min of data recording. Average metabolic rate over these 2 min was calculated using a standard equation (7). We subtracted metabolic power during standing (recorded in a separate 5 min trial) from all walking values to determine net metabolic power. Net cost of transport was calculated by dividing net metabolic power by body weight and speed.

Treadmill. During both open-loop and closed-loop perturbations, subjects walked on a treadmill (Trackmaster 425, Full Vision) that was modified to accept an analog signal to control belt speed. The speed was regulated by a custom treadmill control system (using

Simulink Real-Time Workshop, Mathworks, Natick, MA). The maximum belt acceleration was 0.3 m/s^2. We determined step frequency by attaching pressure-sensitive footswitches to both heels (Multimode Footswitch, Noraxon; Fig. 1A). Step period was calculated from the time between consecutive heelstrikes (sample frequency 100 Hz). To reduce effects of different sensitivities between footswitches, we calculated instantaneous step frequency from a moving average over two steps. Pilot experiments revealed that subjects were uncomfortable with sudden reductions in speed, and so the closed-loop control included a low-pass filter (first order, with 1 s time constant) to the treadmill input voltage to smooth treadmill speed changes. Actual treadmill speed was measured using a reed sensor and a magnet attached to the treadmill flywheel (sample frequency 500 Hz).

Distractor test. We used a modified Stroop test (23) to deter subjects from consciously controlling their gait. This was used in all trials, except when indirect calorimetry equipment was used due to visual obstructions imposed by this equipment. A word for a color (e.g., red) was displayed in a color that could either match the meaning of the word (e.g., printed in red) or not (e.g., printed in blue) for 2 s. Subjects were asked to indicate when the word and its displayed color were in agreement. Subjects generally performed quite well on the test, with only $0.7 \pm 0.5\%$ matches missed (mean $\pm$ SD). Although the distraction appeared to be successful (subjects reported that they were unaware that they were manipulating treadmill speed during the closed loop tests), it also appeared to have little effect on the results, since subsequent testing revealed no differences associated with the presence or absence of the distractor test.

Dimensional analysis. To account for differences in body size, we designed the entire experiment in terms of dimensionless step frequency, speed, and other variables. Frequency and speed were non-dimensionalized by dividing by $\sqrt{g/l}$ and $\sqrt{g \cdot l}$, respectively, where g is gravitational acceleration (9.81 m/s^2) and l is the subject's leg length (m). Metabolic power was non-dimensionalized by dividing by $mg\sqrt{g \cdot l}$, and this was divided by non-dimensional speed to yield cost of transport. For convenience, we report averaged variables in both dimensionless and SI units, re-dimensionalized using the average leg length (0.92 m).

Statistics. For each subject, we fitted the average step frequency response with a two-process model (*Eq. 1*). To average step frequency responses of different amplitudes, we first normalized all responses to
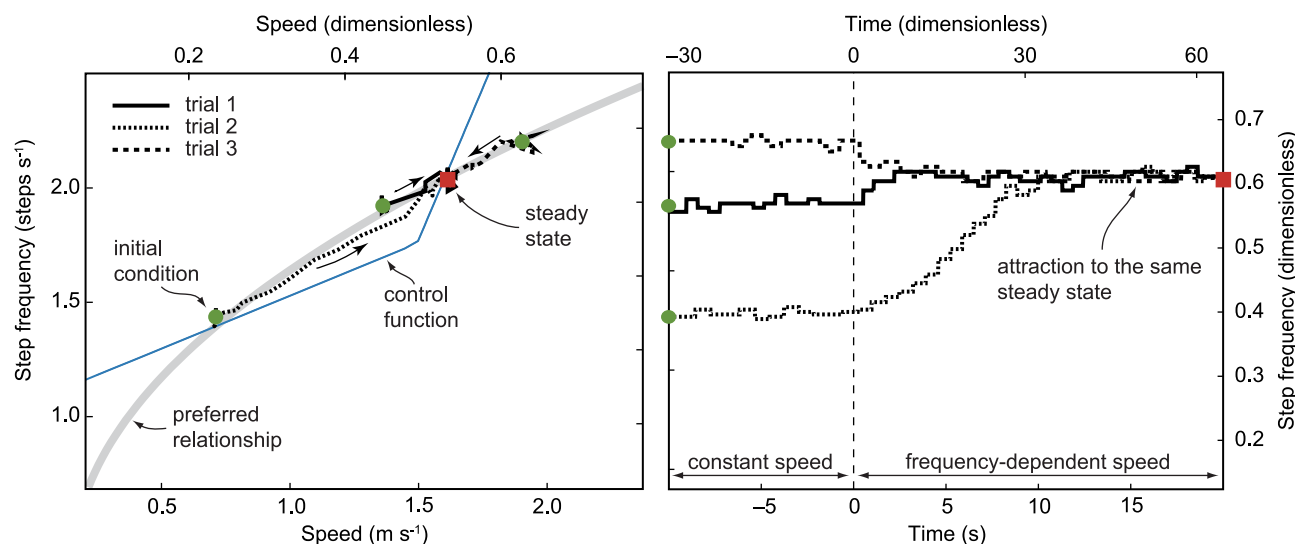

Fig. 3. Responses to closed-loop perturbations for a representative subject. *Left*: when starting from different initial conditions, subjects were rapidly attracted toward the same intersection of the control function (blue line) and their preferred relationship (gray line). *Right*: the same step frequency data (as at *left*) as a function of time. Green circles and red squares indicate 30-s averages of step frequency and speed during the initial condition and during steady state, respectively. This closed-loop behavior is also presented in *movie S1* (see supplemental data at the *Journal of Applied Physiology* website). That subjects were attracted to the upper intersection of the control function and preferred relationship but not the lower one is explained in DISCUSSION, Fig. 5, and the APPENDIX.

a unit change in amplitude. Statistical comparisons were performed using Student's paired *t*-tests. We accepted $P < 0.05$ as statistically significant.

RESULTS

Open-loop perturbations. We found that open-loop perturbations to treadmill speed caused subjects to rapidly adjust their step frequency toward the preferred relationship and then fine-tune it over much longer time scales (Fig. 2). Sudden changes in treadmill speed caused step frequency adjustments to occur with a transient time course that resembled the sum of two exponentially decaying processes (*Eq. 1*). This two-process model described the dynamics of step frequency adjustments of most subjects reasonably well: it accounted for 71–79% of the measured variability in all but one subject (for whom a malfunctioning foot switch caused spurious artifacts in step frequency measurement). The fit was not appreciably improved with alternative models that included more processes or parameters. These fits yielded 95% response times of 1.44 ± 1.14 s (mean ± SD) for the fast component and 27.56 ± 16.18 s for the slow component (equivalent to exponential time constants of 0.48 s for τ_f and 9.20 s for τ_s, respectively). The corresponding amplitudes were 0.66 ± 0.10 and 0.35 ± 0.10, respectively. The fixed time delay, t_0, was 0.81 ± 0.44 s. Both processes were substantially slower than the dynamics of the treadmill, which exhibited negligible time delay and a time constant of 0.42 s in response to commanded open-loop speed changes.

Closed-loop perturbations. We found that, instead of converging on combinations of speed and frequency that minimized energetic cost, subjects remained strongly attracted to their preferred relationship when responding to closed-loop perturbations. They responded by quickly adjusting their step frequency, consistent with the fast dynamics observed in open-loop trials and remained close to their preferred relationship even when treadmill speed changed rapidly. Subjects converged on the intersection of the preferred relationship and the control function from initial conditions both above and below the intersection and with an average error of only 0.3% (Fig. 3; and see *movie S1* available online at the *Journal of Applied Physiology* website). They did not settle on combinations of speed and frequency that minimized net metabolic cost in terms of either metabolic power (cost per unit time) or cost of transport (cost per unit distance). The steady-state combination of speed and step frequency under closed-loop control yielded an average 18% higher cost of transport ($P = 0.038$; Fig. 4) than the minimum along the control function (achievable only with the metronome to guide step frequency). Preferred frequency, 2.06 Hz, was 29% faster than the frequency at which cost of transport was minimized, 1.60 Hz ($P = 2.8 \times 10^{-8}$). Metabolic power at the stable fixed point was also 300% higher than the measured minimum metabolic power ($P = 9.9 \times 10^{-7}$) and occurred at a frequency 77% faster than the corresponding frequency of 1.17 Hz ($P = 1.7 \times 10^{-8}$). Even if subjects initially walked at the minimum cost gait with the help of the metronome, they always converged on a higher cost on removal of the cue, counter to the predicted behavior under direct optimization but consistent with that expected if employing a pre-programmed response.
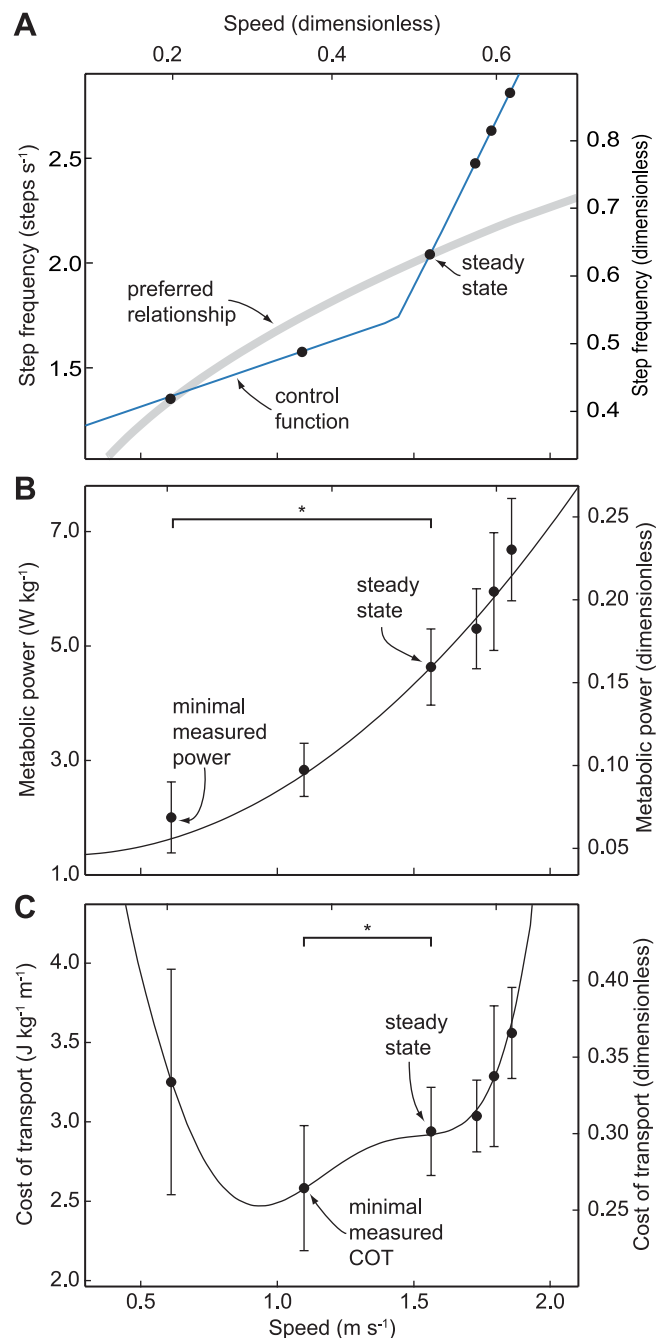

Fig. 4. Metabolic cost of walking at combinations of speed and frequency along the control function. *A*: measurements of energetic cost were made at six different speed-frequency combinations along the control function (●). This was accomplished using the closed-loop treadmill control and a metronome to enforce step frequency. The minimal metabolic power (*B*) and minimal cost of transport (*C*) that we measured along the control function occurred at a different combination of speed and frequency than our subjects preferred when frequency was not constrained by a metronome (labeled as steady state). Data points and error bars are means and SD, respectively, over all subjects. *Statistically significant difference ($P < 0.05$). Black lines denote curve fits for illustration only.

DISCUSSION

We found transient responses to have two underlying processes, one fast and one slow. With open-loop changes in treadmill speed, the fast process dominated the response so that

step frequency adjustments were two-thirds complete in <2 s. That process tended to drive step frequency toward the normal preferred relationship much more quickly than would be expected from direct optimization. Moreover, the fast attraction to the preferred relationship persisted even during unusual closed-loop conditions that rendered the resulting step frequency energetically suboptimal. These fast process characteristics suggest that the gait patterns that normally minimize metabolic cost are pre-programmed within the neural circuitry that controls locomotion.

The slow process underlying the transient response took ~30 s to reach 95% completion (20 times slower than the fast process) and accounted for a much smaller but nonetheless important fraction of the overall step frequency adjustment. We interpret its time course as consistent with that expected of direct optimization due to the relatively slow response times of direct metabolic cost sensors (9, 14, 18, 20, 24) as well as the need to assess steady-state expenditure and iteratively adjust step frequency over multiple steps.

The fast process underlying step frequency selection appears to be persistent and consistent, as evidenced by the strong attraction to the normally preferred speed-frequency relationship even under unusual closed-loop conditions. We further tested its behavior by applying different control functions designed to produce a variety of unusual but predictable behaviors. These included attraction to different stable intersections, repulsion from an unstable intersection, and oscillations. The predicted stability of an intersection, referred to as a fixed point in nonlinear dynamics (36), depends on whether the control function has a steeper or shallower slope than the preferred relationship at the intersection (Fig. 5, *A* and *B*; see APPENDIX for mathematical details). Oscillations are predicted to occur when the control function has a negative slope at the intersection (Fig. 5*C*). Indeed, we found that subjects would quickly converge to different combinations of speed and step frequency along the preferred relationship depending on where the stable intersection was placed (Fig. 6*A* and see *movie S1* available online at the *Journal of Applied Physiology* website). In unstable cases, the closed-loop interaction resulted in speed progressing away from the initially preferred gait. The subjects would slow to a stop if starting with an initial speed slower than the unstable fixed point, or increase speed to a run if

starting above the unstable fixed point (Fig. 6*B* and see *movie S2* available online at the *Journal of Applied Physiology* website). In the case of oscillatory behaviors, the step frequency and speed persistently fluctuated about the intersection (Fig. 6*C* and see *movie S3* available online at the *Journal of Applied Physiology* website). These behaviors occurred for all subjects and in all trials for which stable fixed points, unstable fixed points, or oscillations were predicted. It is important to recognize that these behaviors are not simply a consequence of the treadmill adjusting speed based on the different control functions; they also require the subjects to persistently and rapidly change step frequency toward their preferred relationship.

It is interesting that subjects did not override the normal preferred relationship and converge on a lower metabolic cost. Humans can volitionally walk with combinations of speed and step frequency other than preferred, and our subjects had little difficulty with gaits along the control function when matching the beat of a metronome. If they had disregarded their preferred relationship, then direct optimization would be expected to slowly converge on a lower-cost gait along the control function. That result might also have been attained had subjects altered the preferred relationship itself, for example, by shifting it to yield a lower-cost, stable fixed point. Subjects did experience the lower-cost gaits with the help of a metronome (Fig. 4). But on removal of that cue, they were quickly attracted toward their normally preferred step frequency and were apparently unable to suppress that tendency within the few hours they were exposed to the closed-loop conditions. Both their earlier experience with a lower-cost gait and a hypothesized inclination to optimize metabolic cost appear to be outweighed by a stronger and faster attraction to the preferred relationship. This was true even when the preferred gait was rendered energetically suboptimal or used to produce unusual walking patterns, such as persistent oscillations in speed and frequency (Fig. 6).

Although the dynamics of the fast pre-programmed response are mathematically simple, the underlying physiological mechanisms may be considerably more complex. A variety of inputs, including proprioceptors, vision, and other sensors, could each contribute to the estimation of walking state (21) so that the CNS can use them to rapidly recall a stored association
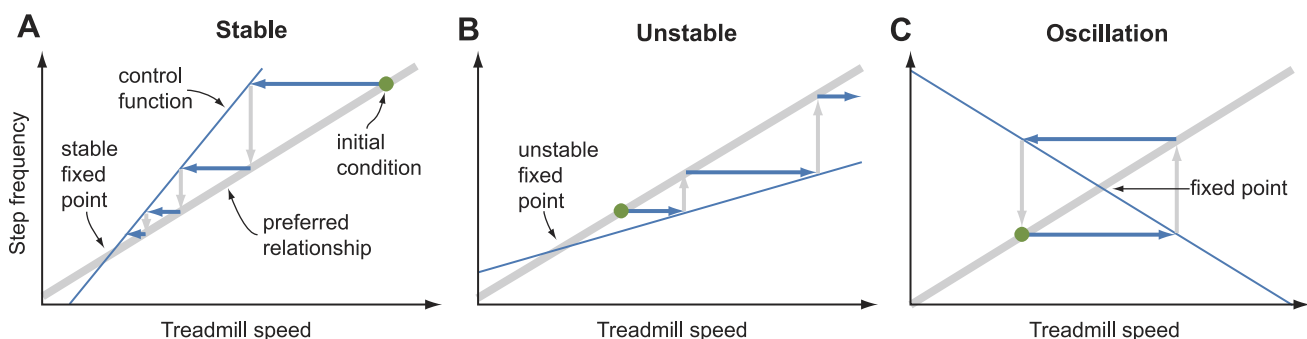

Fig. 5. Conceptual illustration of the predicted behavior around intersections of the preferred relationship and the control function, termed "fixed points." The initial condition (green circle) can be considered as a perturbation away from the fixed point. After the frequency-dependent speed control is engaged, treadmill speed will change toward the speed defined by the control function. In response to this changing speed, subjects change their step frequency toward their preferred relationship. *A*: when the slope of the control function is greater than the slope of the preferred relationship, perturbations are attenuated, thus attracting the subject toward the stable fixed point. *B*: when the slope of the control function is shallower than the slope of the preferred relationship, perturbations are amplified, thus repelling the subject away from the unstable fixed point. *C*: oscillations about the fixed point are predicted when the ratio of the slopes of the preferred relationship and the control function is negative.
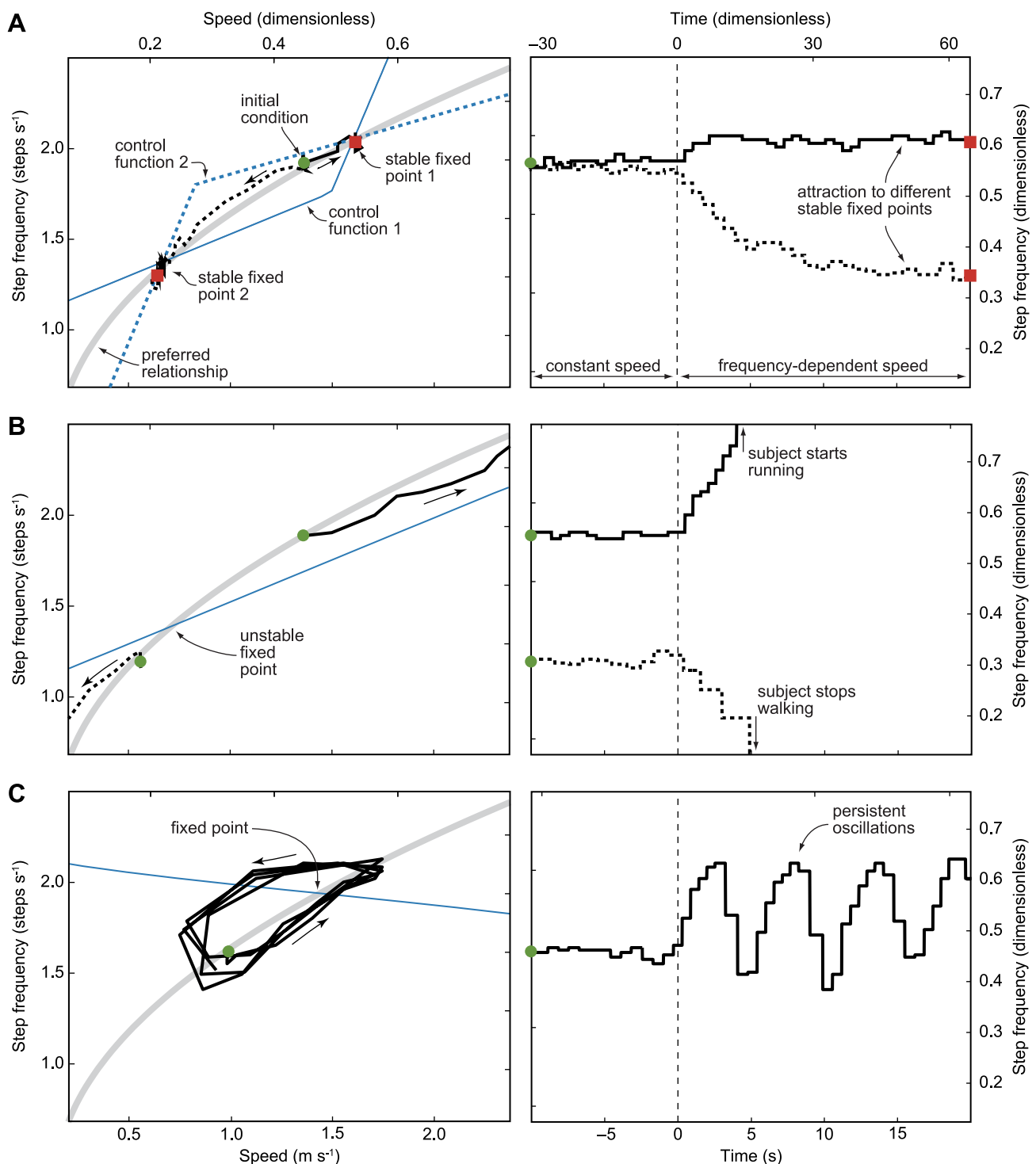
Fig. 6. Representative data from a single subject illustrating the closed-loop perturbation response to various control functions. The same step frequency data is shown as a function of speed (*left*) and as a function of time (*right*). *A*: stable fixed points. Both of the illustrated control functions intersect the preferred relationship twice, but only one intersection is stable for each control function, whereas the other intersection is unstable (Fig. 5). Starting from the same initial condition, subjects were rapidly attracted toward the different stable fixed points for the different control functions. Green circles and red squares indicate 30-s averages of step frequency and speed during the initial condition and during steady state, respectively. *B*: unstable fixed point. Subjects were rapidly repelled from the intersection of the control function and their preferred relationship. *C*: oscillatory behavior. A control function with a negative slope resulted in persistent oscillations around the fixed point. The unstable fixed-point and oscillatory behaviors are also presented in *movies S2* and *S3* (available online at the *Journal of Applied Physiology* website).

between speed and step frequency. This stored program may be embedded within reflexes and other feedback circuits in the form of feedback gains or appropriate parameters within gait pattern generators (28). However, the rapid response to treadmill perturbations does not appear to be a stumbling reaction reflex, which appears to be elicited only by much faster accelerations (11) than the 0.3 m/s² used in our experiments.

The observed responses may also have a contribution from purely biomechanical mechanisms. For example, the treadmill acceleration likely forces an early termination of the swing phase and thus an immediately faster step (22). But this cannot explain all of the human adjustments, which largely commenced after the treadmill had nearly completed its speed changes and continued long after the treadmill reached steady state. Another possible biomechanical contribution may come from coupled dynamics between the legs that induce a biomechanical relationship between speed and step frequency (10, 25). Whatever the actual mechanisms underlying the observed responses, they appear to be sufficiently automatic that subjects are unable to suppress them volitionally.

The pre-programmed preferred relationship between speed and frequency is likely not unique but may instead depend on context. For example, Bertram and Ruina (6) measured the preferred speed-frequency relationship with different constraints on speed, step frequency, or step length, and found these to yield different preferred speed-frequency relationships, all consistent with minimizing cost of transport. Perhaps humans recognize different contexts and, given sufficient experience with them, learn different programs as appropriate. We would therefore expect that different speed-frequency constraints, or other contexts, would eventually yield different programmed gaits given sufficient time for adaptation.

It appears that pre-programming facilitates rapid selection of the approximately optimal step frequency, with only a small amount of fine tuning performed subsequently and much more slowly. A disadvantage of pre-programming is that it must assume a context under which the preferred step frequency may be predicted. Consequently, we could render the pre-programmed optimal step frequency incorrect using our unusual closed-loop control function. Perhaps, with continued practice, our subjects could have eventually adapted or overridden their preferred relationship to achieve the correct optimum. Although the time scale of this adaptation is unknown, it seems sensible that the CNS should adapt no slower than the time scale of the body itself as it changes through development and aging. But regardless of how pre-programmed gaits are acquired, they appear to enable humans to rapidly select their normally preferred step frequency, whereas other processes slowly fine tune the gait toward the energetic optimum.

APPENDIX

To perform a local stability analysis, we first linearized both the control function and the preferred relationship in the neighborhood of their intersection, yielding two linear functions:

$$f = m_c v + b_c \qquad (A1)$$

$$f = m_p v + b_p \qquad (A2)$$

where f is step frequency, v is treadmill speed, each m is a slope, and each b an intercept. *Equations A1* and *A2* are the control function and preferred relationship, respectively, distinguished by corresponding subscripts c and p. Assuming step changes in treadmill speed, at

iteration k, treadmill speed $v(k)$ is defined by the control function and the current step frequency $f(k)$:

$$v(k) = \frac{f(k) - b_c}{m_c} \qquad (A3)$$

Because subjects will adopt the step frequency given by the preferred relationship at each speed, at iteration $k + 1$, the step frequency $f(k + 1)$ is the consequence of the previous iteration's treadmill speed $v(k)$:

$$f(k + 1) = m_p v(k) + b_p \qquad (A4)$$

Combining *Eqs. A3* and *A4* demonstrates that the frequency of the next iteration is a function of step frequency of the previous iteration:

$$f(k + 1) = m_p \frac{f(k) - b_c}{m_c} + b_p \qquad (A5)$$

A fixed point (denoted by an asterisk) occurs when the step frequency of the next iteration is equal to the step frequency of the previous iteration. This occurs at the speed where the control function and preferred relationship intersect; thus:

$$\frac{f^* - b_c}{m_c} = \frac{f^* - b_p}{m_p} \qquad (A6)$$

Rewriting *Eq. A6* yields an expression for the frequency at the fixed point:

$$f^* = \frac{b_c m_p - b_p m_c}{m_p - m_c} \qquad (A7)$$

The local asymptotic stability of a fixed point is determined by whether a small frequency perturbation away from the fixed point decays or grows over time. This is evaluated by substituting step frequency in *Eq. A5* with a perturbation ε away from the fixed point f^*:

$$f^* + \varepsilon(k + 1) = m_p \frac{f^* + \varepsilon(k) - b_c}{m_c} + b_p \qquad (A8)$$

Combining *Eqs. A7* and *A8* and cancelling terms yields:

$$\varepsilon(k + 1) = \frac{m_p}{m_c} \varepsilon(k) \qquad (A9)$$

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