Fast visual prediction and slow optimization of preferred walking speed

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O'Connor SM, Donelan JM. Fast visual prediction and slow optimization of preferred walking speed. *J Neurophysiol* 107: 2549–2559, 2012. First published February 1, 2012; doi:10.1152/jn.00866.2011.—People prefer walking speeds that minimize energetic cost. This may be accomplished by directly sensing metabolic rate and adapting gait to minimize it, but only slowly due to the compounded effects of sensing delays and iterative convergence. Visual and other sensory information is available more rapidly and could help predict which gait changes reduce energetic cost, but only approximately because it relies on prior experience and an indirect means to achieve economy. We used virtual reality to manipulate visually presented speed while 10 healthy subjects freely walked on a self-paced treadmill to test whether the nervous system beneficially combines these two mechanisms. Rather than manipulating the speed of visual flow directly, we coupled it to the walking speed selected by the subject and then manipulated the ratio between these two speeds. We then quantified the dynamics of walking speed adjustments in response to perturbations of the visual speed. For step changes in visual speed, subjects responded with rapid speed adjustments (lasting <2 s) and in a direction opposite to the perturbation and consistent with returning the visually presented speed toward their preferred walking speed, when visual speed was suddenly twice (one-half) the walking speed, subjects decreased (increased) their speed. Subjects did not maintain the new speed but instead gradually returned toward the speed preferred before the perturbation (lasting >300 s). The timing and direction of these responses strongly indicate that a rapid predictive process informed by visual feedback helps select preferred speed, perhaps to complement a slower optimization process that seeks to minimize energetic cost.

visual feedback; energetics; locomotion

OF ALL THE POSSIBLE WAYS TO WALK, people prefer specific patterns. For example, rather than use our full range of possible walking speeds, we prefer a narrow speed range and will switch to a running gait if we have to move much faster (Bertram 2005; Bertram and Ruina 2001; Bornstein and Bornstein 1976; Margaria 1938; Ralston 1958; Zarrugh et al. 1974). Within a speed, we prefer to use specific combinations of other gait parameters such as step frequency and step width (Donelan et al. 2001; Elftman 1966). Although there is strong evidence that these preferred gaits minimize energetic cost during long bouts of steady-state walking (Bertram 2005; Donelan et al. 2001; Elftman 1966; Ralston 1958), the specific neural control mechanisms underlying economical gait selection are currently unknown.

People may converge on their preferred gaits by directly sensing metabolic rate and dynamically adapting their gait to continuously maximize gait economy (Fig. 1). In particular, people generally minimize the metabolic cost of transport, defined as the metabolic rate per unit of walking speed, and

therefore optimizing cost of transport would require sensing both speed and metabolic rate. Estimates of walking speed could be rapidly attained from visual, proprioceptive, and other feedback. However, the potential direct sensors of metabolic cost, such as central and peripheral chemoreceptors and group IV muscle afferents, are reported to require at least 5 s to produce a physiological response to a stimulus (Bellville et al. 1979; Coote et al. 1971; Kaufman and Hayes 2002; Smith et al. 2006). Even without these sensing delays, considerable time would still be required for an optimization process to use this metabolic information to iteratively adjust gait from step to step, and thus would only gradually converge to the optimal pattern. If this process were used to select preferred speed, for example, adaptations would be expected to occur over tens of seconds or longer due to the compounded effects of sensing and iterative adjustments. However, everyday walking is made up of a series of short bouts, most frequently lasting only 20 s (Orendurff et al. 2008). Even much longer bouts may require rapid economical adjustment of gait to respond to constantly changing terrains and environments. Direct optimization is therefore unlikely to keep up with the continuously changing situations in which we move.

A potentially faster mechanism would be to rely on indirect sensory feedback to predict walking patterns that minimize cost of transport and then use this prediction to help select the preferred gait (Fig. 1). Based on relationships learned over time, sensory feedback from vision and other pathways could be used to rapidly predict the energetic consequences of specific gait patterns while also considering environmental and task constraints such as terrain and maintaining balance (Mercier et al. 1994; Snaterse et al. 2011; Thorstensson and Roberthson 1987). For example, prior knowledge of the association between energy expenditure and walking speed would allow one to immediately predict the energetically optimum adjustments to speed based only on the currently sensed speed. The visual pathways are known to be partially responsible for sensing and making adjustments to walking speed: increasing visual flow rate relative to the actual walking speed elicits significantly slower average preferred speeds, and vice versa (De Smet et al. 2009; Mohler et al. 2007a; Prokop et al. 1997). However, it is still unclear whether vision is used for the rapid gait adjustments that are indicative of indirect prediction, since these studies only used slow visual perturbations that cannot identify the dynamics of the processes involved.

The use of both indirect prediction and direct optimization is a sensible strategy for selecting energetically optimal gaits, since these two processes would have complementary strengths and weaknesses. Direct optimization could accurately minimize energetic cost because it relies on the actual sensed metabolic rate, but it has the drawback of a relatively slow response time. Information from other body senses, such as
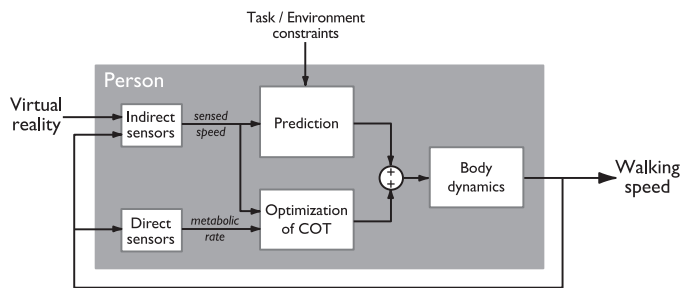
Fig. 1. Conceptual diagram illustrating the person as a dynamic system that selects the preferred walking speed given environmental and task constraints. We hypothesize that there are 2 physiological processes, indirect prediction (fast) and direct optimization (slow), that operate on different time scales and underlie the selection of preferred walking mechanics. Indirect prediction uses sensed speed to predict economical walking speed adjustments based on prior experience. Direct optimization uses sensed metabolic rate and speed to estimate the cost of transport (COT) and adapts walking speed to minimize it. The dynamics of these 2 processes can be tested by decoupling the relationship between actual and sensed walking speed through the use of virtual reality and applying perturbations to visually presented speed.

vision, proprioception, and the vestibular system, could be available much more rapidly and could be used to predict optimal gait changes on short time scales. However, indirect prediction would be less accurate by relying on prior experience and indirect means to reduce energetic cost. Evidence for these two processes has been demonstrated for step frequency adjustments, where sudden perturbations to walking speed cause subjects to first rapidly adjust step frequency toward the most economical frequency at that speed and then fine-tune it over longer time scales (Snaterse et al. 2011). The fine-tuning can be explained by an optimization process, but the rapid adjustment, which constitutes a majority of the adaptation, is more consistent with a preprogrammed behavior. Although these results suggest that indirect prediction is used to rapidly select preferred gaits, the underlying sensory mechanisms have not yet been identified.

The purpose of this present study was to understand the mechanisms underlying the selection of preferred gaits. Our general hypothesis was that a fast predictive process and a slow direct optimization process govern the selection of preferred walking speed. To test the first part of this hypothesis, we leveraged prediction's expected dependence on indirect sensory feedback and perturbed visual flow using virtual reality. We anticipated that in response to sudden visual flow rate perturbations, indirect prediction would cause subjects to rapidly adjust walking speed in a direction consistent with returning the visually presented speed back toward the preferred walking speed. Such a response would normally be consistent with cost of transport minimization but in this case would cause subjects to move away from their normally preferred speed based on false visual feedback. We also anticipated that subjects would gradually reject sustained visual perturbations and return back to the preferred speed before the perturbation, either due to a slower optimization process that seeks to minimize the actual cost of transport or due to sensory reweighting that recalibrates the discordant visual feedback. Within our analysis, we use the terms "preferred walking speed" and "energetically optimal walking speed" interchangeably due to the many studies demonstrating that people consistently prefer a speed that minimizes their metabolic energy cost per unit distance traveled (Bertram 2005; Bertram and

Ruina 2001; Browning and Kram 2005; Margaria 1938; Ralston 1958; Zarrugh et al. 1974).

MATERIALS AND METHODS

To address our hypothesis, we manipulated the speed visually presented to subjects while allowing them to freely adjust their actual speed. To accomplish this, we used a self-paced treadmill surrounded by a virtual reality screen that projected a moving hallway scene (Fig. 2A and Supplementary Movie 1). (Supplemental data for this article is available on the *Journal of Neurophysiology* website.) Rather than manipulating the hallway speed directly, we coupled the speed of visual flow to the walking speed selected by the subject and then manipulated the ratio between these two speeds. This speed ratio, which can be thought of as a gain on visual flow rate, is defined as

$$\text{Visual speed} = (\text{speed ratio}) \times (\text{walking speed}) \qquad (1)$$

When the speed ratio is less than one, for example, visual feedback would suggest to the subject that they are moving slower than their actual speed. Visually presented speed can then be perturbed through changes to the speed ratio, yet remain under the subject's control; subjects could always increase their visually presented speed by simply walking faster (Fig. 2B). This helped to ensure that perturbations to visual flow rate were actually perceived by subjects as changes in their own walking speed.

We used two types of experimental perturbations to identify the mechanisms underlying the selection of preferred walking speed. The first perturbation scheme applied step changes in visually presented speed to determine whether the adjustments in actual speed are consistent in timing and direction with those attributed to indirect prediction and/or direct optimization. The amplitudes of the adjustments also provide an estimation of the visual contribution to the predictive selection of walking speed within our experiment. If only indirect prediction was used, subjects would rapidly adjust walking speed in a direction consistent with returning the visually presented speed back toward the preferred walking speed and the adjustments would persist for the duration of the perturbation (Fig. 2C). If direct optimization alone was used, or if vision was not a sensory input into the predictive process, we would see no response to visual perturbations. We predicted a combination of these processes as a third possibility: indirect prediction will cause subjects to rapidly change speed in response to a step input, and a slower process will gradually return subjects back to their preferred speed over time. However, it should be noted that this experimental paradigm cannot distinguish the source of the slow process, and we leave open the possibility that this process could be explained by the direct optimization of the cost of transport, sensory reweighting of visual stimuli, or a combination of both.

The second type of perturbation used sinusoidal changes in the speed ratio to provide a secondary measure of the visual contribution to predictive speed selection within our experiment (Fig. 2D). We expected the responses to the sinusoidal perturbations to be dominated by indirect prediction if the frequency of the sinusoidal perturbations was fast relative to the dynamics of the slow process. If the visual information provided were the only input into the predictive process, a speed ratio varying between 0.5 and 2 would require subjects to adjust their walking speed between twice and one-half their preferred speed to maintain a visually presented speed that matches the preferred walking speed. We expected more modest adjustments, since other sources such as proprioception would contribute to sensed speed and because the self-motion illusion created through virtual reality is imperfect (Prokop et al. 1997). Although sinusoidal perturbations have already been shown to produce changes in walking speed (Prokop et al. 1997), including them in this experiment served the dual purpose of validating those results while confirming that our particular virtual reality system can induce measureable speed adjustments.
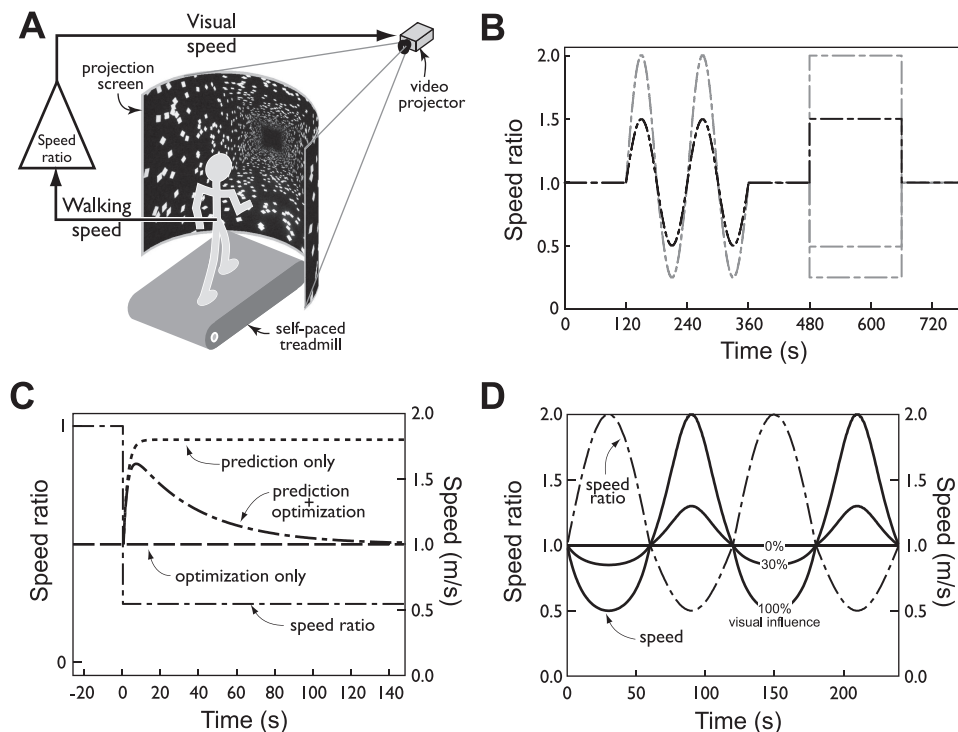
Fig. 2. Experimental paradigm and predictions. *A*: a virtual reality system applies visual perturbations through a projection display and measures changes in walking speed on a self-paced treadmill. The virtual environment consists of a dark hallway tiled with randomly placed white squares. Subjects are able to freely select their walking speed via a feedback control system that measures the subject's fore-aft location and adjusts treadmill speed to keep the subject centered on the treadmill. The visually presented speed of motion through the virtual environment is coupled to the walking speed selected by the subject through a proportional "speed ratio," with the value equal to 1 for control conditions. *B*: experimental trials consisted of a series of sinusoidal and step perturbations in speed ratio with control conditions in between. Superimposed profiles of these perturbations are shown for all 4 experimental trials. *C*: the theoretical effects of sudden perturbations in speed ratio on self-selected walking speed can be represented by 2 processes that act on different time scales. A rapid initial response to step changes in speed ratio in a direction opposite to the change in speed ratio will support the hypothesis that vision is used for predictive control. If direct optimization alone were used, we would expect no response to visual perturbations. We predict a combination of these two strategies: indirect prediction will cause subjects to rapidly change speed in response to a step input but will gradually return back to their preferred speed over time. *D*: sinusoidal changes can be used to determine the degree of visual influence on predictive selection of walking speed. If only vision were used, subjects would modify walking speed to maintain a constant visual flow rate (walking speed would have to double for a speed ratio of 0.5). See also Supplementary Movie 1.

Experiment. Ten volunteers participated in this study (6 male, 4 female; age 25.9 ± 3.9 yr; body mass 70.6 ± 12.1 kg; leg length 0.93 ± 0.05 m; means ± SD). All were healthy adults with no known visual conditions or impairments affecting daily walking function. Simon Fraser University's Office of Research Ethics approved the protocol, and all subjects gave written informed consent before participation.

Subjects walked on a treadmill that allowed them to freely select their walking speed (Fig. 2*A*). We implemented this self-paced feature by designing a feedback controller that measured subject position via reflective markers (Vicon Motion Systems) placed at the sacrum and adjusted treadmill speed to minimize the fore-aft displacement from the center of the treadmill. The control system was designed to provide prompt responses to changes in walking speed while maintaining a smooth feeling during steady-state walking (Lichtenstein et al. 2007). We determined instantaneous walking speed from the sum of instantaneous treadmill speed and the subject speed relative to the treadmill.

We applied visual perturbations through a wide field-of-view virtual reality projection system placed around the treadmill (Fig. 2*A*). The virtual scene consisted of a dark hallway with the floors, ceiling, and walls tiled with randomly placed white squares. This setup was modeled after previously used systems that have been shown to successfully induce adjustments to gait variability and walking speed (O'Connor and Kuo 2009; Prokop et al. 1997). The virtual hallway speed was coupled to walking speed via a proportional speed ratio (*Eq. 1*) and streamed to the projection system by the treadmill controller. To increase the sense of immersion, subjects wore eyewear

designed to block the edges of the screen as well as headphones playing noise to mask auditory cues that change with treadmill speed. Subjects additionally completed an auditory memory task during the experimental trials to distract them during the visual perturbations. This task involved listening for a series of low and high pitch tones (500 and 1,200 Hz), presented in random order every 3 s, and verbally reporting whether the most recent tone was the same as the one before it. For all trials, subjects were instructed to look forward and use the visual information as naturally as possible as they walked toward the end of the hallway at a comfortable pace.

The experiment was completed over two sessions occurring on consecutive days. During the first day of testing, subjects were familiarized with the self-paced treadmill and the virtual reality environment, all with congruent visually presented and actual walking speeds (speed ratio = 1). Subjects walked for a total of 40 min, over which visual feedback from the display, auditory background noise, and then the distractor test were progressively added. The second day focused on measuring responses to visual perturbations. Subjects began the second session by completing an abbreviated training protocol (speed ratio = 1) lasting 20 min and then completed 4 experimental trials. The background noise in conjunction with the audio distractor test was used in all subsequent experimental trials. Each of the 4 experimental trials consisted of a series of sinusoidal and step perturbations in speed ratio lasting 13 min (Fig. 2*B*). Each trial manipulated speed ratio as follows: 2 min at a speed ratio of 1, 4 min of sinusoidal changes in speed ratio with a period of 120 s, 2 min at a speed ratio of 1, a sudden step change in speed ratio maintained for 3 min, and 2 min at a speed ratio of 1. We used speed

ratio sinusoids of two different ranges: the first ranged from 0.5 to 1.5, and the second from 0.25 to 2. The values of the step perturbations to speed ratio were 0.25, 0.50, 1.5, and 2.0. The step changes to the speed ratio signal were slightly smoothed, taking 0.2 s to complete, so that changes in visually presented speed did not appear abrupt. The amplitudes of the step and sinusoidal perturbations were presented in random order for each trial. Short breaks (5–10 min) were given after every trial.

Analysis. We used standard techniques from system identification to quantify the dynamics of speed adjustments in response to step and sinusoidal changes in speed ratio. System identification is a general term to describe algorithms for constructing mathematical models of dynamical systems from measured input-output data (Ljung 1987). The hypothesized responses to visual flow perturbations applied at the preferred walking speed can be most simply represented as the combination of two parallel processes acting on different time scales, one that immediately adjusts speed in the opposite direction of the visual perturbation (fast process) and another that attempts to reject these adjustments over a longer time scale (slow process) (see Fig. A1). A mathematical representation of our model, expressed as a transfer function in the Laplace domain, takes the form

$$Y(s) = \left(\frac{-a \cdot G(s) \cdot P(s)}{1 + G(s) \cdot P(s) + G(s) \cdot O(s)} \right) X(s), \qquad (2)$$

where s is the Laplace variable, $X(s)$ is the input (change in speed ratio), $Y(s)$ is the output (change in normalized walking speed), $G(s)$ represents the body dynamics, $P(s)$ represents the dynamics of a fast control process that responds to the speed ratio perturbations, and $O(s)$ represents the dynamics of a slow control process that rejects these adjustments (see APPENDIX). The parameter a represents the magnitude of the relative weighting of visual speed information compared with speed information from other sensory sources and is limited to a range between 0 and 1. We chose the transfer functions $G(s)$, $P(s)$, and $O(s)$ to produce the hypothesized rapid response to visual perturbations, and its gradual rejection, with the fewest number of parameters (see APPENDIX), where

$$G(s) \cdot P(s) = \frac{1}{\tau_f s}, \; G(s) \cdot O(s) = \frac{1}{\tau_s s^2},$$
$$Y(s) = \left(\frac{-a\tau_s s}{\tau_f \tau_s s^2 + \tau_s s + \tau_f} \right) X(s). \qquad (3)$$

Here, the body dynamics $G(s)$ and indirect prediction P(s) are combined to yield a "fast process" that quickly adjusts speed in response to the input, and G(s) and O(s) are combined to yield a "slow process" that adjusts speed to reject these changes over longer time scales. The parameters τ_f and τ_s represent timing parameters for the fast and slow processes and have units of seconds and seconds squared, respectively. These timing parameters affect the poles of the closed-loop model and thus the dynamics of the overall response to the input.

We used the step perturbation trials to identify the magnitude of the visual weighting, the timing parameters for the fast and slow processes, and most importantly, the dynamics of the overall closed-loop behavior. We quantified the timing parameters of the fast and slow processes, τ_f and τ_s, for the purposes of fitting the input-output experimental data to our model structure. However, the overall dynamics of the system are determined by the closed-loop behavior of the individual processes acting in parallel, which we quantified using response times. The response time of the initial rapid behavior is defined as the estimated time to achieve 95% of the initial change in walking speed after the step change in speed ratio. The slow behavior response time is the estimated time to return to within 5% of the original speed before the perturbation. We also quantified the amplitude of the visual weighting parameter a, where a value of 0 would indicate that vision is insensitive to perturbations of speed ratio. We identified these three model parameters using the step changes in

speed ratio as the input to the model and the normalized walking speed responses as the output. To prepare the input data for this analysis, we subtracted 1 from the speed ratio to give change in speed ratio. To prepare the output data, we divided the walking speed by the measured preferred walking speed before the perturbation and subtracted 1 from this value to give change in normalized walking speed. Each trial was aligned in time to start at the onset of response in walking speed, and onset delays were recorded for each trial. We computed the average onset delay from individual trials and determined significance using *t*-tests.

We also used the sine perturbations to separately identify the visual weighting parameter, *a*, and quantify the contribution of vision to the predictive selection of walking speed. For example, an amplitude of 0.3 would roughly suggest that vision accounts for 30% of the sensory resources used for predictive speed control. We identified this model parameter using the sine wave speed ratio perturbations as the input and the normalized walking speed responses as the output. Because sine perturbations do not excite the model dynamics sufficiently to re-identify all model parameters, the timing parameters found from the step perturbations were assumed to be fixed. The input and output data were prepared in the same manner as for the step perturbations, except that we first detrended the measured speed during the sinusoidal perturbations. Although the fast-process amplitude may be identified from the step-response data alone, we also used the sine perturbations to facilitate comparison with previous sine perturbation experiments. Even though this method requires the assumption of fixed timing parameters, we expected that sine perturbations might still provide a more accurate estimation of the visual weighting, because speed adjustments were more reliably induced from these perturbations and because subjects reported less awareness that the sinusoids were occurring.

The identified parameters minimized the sum of the squared error between the model predictions, based on the step and sine inputs, and the measured walking speed adjustments. To implement this system identification and to generate estimates and confidence bounds on the parameter values, we used MATLAB's idgrey.m and pem.m functions.

RESULTS

The average preferred walking speed before the visual perturbations was 1.40 ± 0.03 m/s (mean ± 95% confidence interval), which is near the value of 1.33 m/s that has been previously reported to minimize the cost of transport (Browning and Kram 2005; Zarrugh et al. 1974). We also found the audio distractor test to have no significant effect on preferred walking speed ($P = 0.78$, paired *t*-test) compared with walking with background noise alone during training.

In response to step changes in speed ratio, subjects rapidly adjusted walking speed and then exhibited longer term adjustments that gradually returned walking speed toward the steady-state values before the perturbation (Fig. 3, *A* and *B*). The directions of the initial speed changes were consistent with an attempt to minimize the difference between the visually presented speed and the subjects' preferred walking speed. For example, when a step decrease in speed ratio caused a step decrease in presented speed, subjects rapidly increased their walking speed, bringing the presented speed closer to the preferred value at the expense of their actual walking speed. However, the long-term adjustments gradually rejected the effects of the visual perturbation and returned the walking speed toward the originally preferred value even though the visually presented speed remained very different from the actual walking speed.
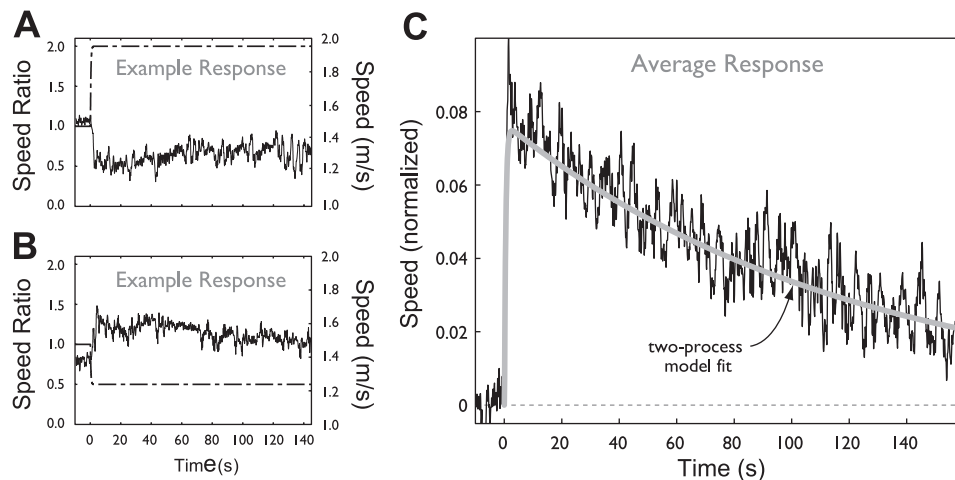
Fig. 3. Adjustments in walking speed in response to step perturbations of speed ratio. *A* and *B*: subjects rapidly adjust walking speed (solid black lines) in a direction consistent with returning the visually presented speed back toward the preferred walking speed and then gradually returned toward their preferred speed before the perturbation. Data shown in *A* and *B* are representative individual trials. *C*: this behavior is well described by a 2-process model fit (gray line) with response times of 1.4 ± 0.3 s for the initial response and 365.5 ± 10.8 s for the gradual return to steady state. The magnitude of the visual weighting parameter is 0.10 ± 0.04 and suggests that vision accounts for ~10% of the sensory drive into prediction within our step perturbation experiment. Although the fit was performed on normalized walking speed from individual trials, the data shown is the average over all trials. Negative adjustments in walking speed, as in *A*, were first inverted in the positive direction before averaging. Values are means ± 95% confidence interval (CI).

Subject responses are well described by two parallel processes acting on different time scales (Fig. 3*C*). Based on the measured dynamics, the estimated response times of the initial response and the gradual return to steady-state differed by more than two orders of magnitude, with values of 1.4 ± 0.3 and 365.5 ± 10.8 s, respectively. These dynamics are a result of the interaction of the two processes acting in closed-loop combination. The identified timing parameters associated with the fast and slow processes was 0.5 ± 0.1 s and 59.1 ± 12.0 s^2, respectively. The initial response occurred after an average onset delay of 5.7 ± 2.5 s, consistent with other experimental findings that induce the sensation of movement through sudden visual stimuli (Mohler et al. 2005; Riecke et al. 2005; Tanahashi et al. 2007). The amplitude of the visual weighting parameter was 0.10 ± 0.04, which corresponds to an average initial change in walking speed of 0.10 m/s and suggests that the visual feedback provided in this step perturbation experiment accounted for 10% of the sensory drive into the predictive selection of walking speed. The two-process model (*Eq. 3*) explained 60% of the average subject behavior for the step perturbations (R^2 = 0.60). We consider this a respectable fit given that the steady-state variability in speed was large relative to the speed changes induced by the visual perturbations. Furthermore, an analysis of the residual errors (not shown) indicated that the two-process model captured the dynamics of interest: the errors were randomly distributed around zero and showed no particular pattern with time.

In a subset of trials, subjects showed a reduced sensitivity to the step perturbations. Although subjects responded to the step changes in speed ratio during a majority of the trials, subjects did not respond at all in 5 of the 40 trials (Fig. 4*A*). A third type of response exhibited a rapid initial adjustment in speed that was quickly rejected and occurred in an additional 5 trials (Fig. 4*B*). We examined whether these responses were correlated with the subject, perturbation direction, perturbation amplitude, and trial order. We found that 4 of 5 nonresponses occurred for smaller step changes in speed ratio (1.5 and 0.5). Rejection responses only occurred during the last two trials of the experiment. We therefore interpreted the reduced sensitivity to visual perturbations as subjects either ignoring the smaller visual perturbations or learning to discard them after several trials and excluded those trials from the step perturbation analysis.

The sinusoidal perturbations to speed ratio caused corresponding out-of-phase sinusoidal changes to walking speed: when speed ratio increased, walking speed decreased, and vice versa (Fig. 5*A*). System identification revealed that the visual feedback provided in this sinusoidal perturbation experiment accounted for 5.8% of the sensory drive into the predictive selection of walking speed (Fig. 5*B*). This value was derived from the visual weighting parameter, 0.058 ± 0.001, identified from the sinusoidal perturbation data with the timing parameters fixed on the basis of the step responses. Given the average preferred walking speed of 1.40 m/s, this means that average
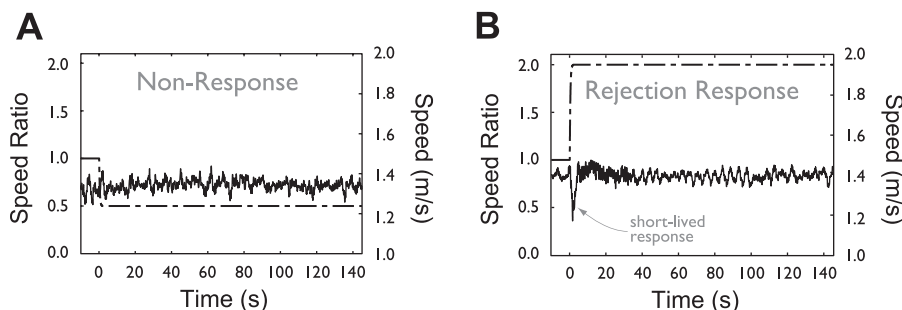

Fig. 4. In a subset of trials, subjects showed a reduced sensitivity to the step perturbations in speed ratio. *A*: in 12.5% of trials, subjects did not respond to the visual perturbations. *B*: in a second 12.5% of trials, subjects rapidly adjusted walking speed and then rapidly rejected the change. Data shown are representative individual trials.

Fig. 5. Adjustments in walking speed in response to sinusoidal perturbations of speed ratio. *A*: in response to continuous sinusoidal perturbations of speed ratio, subjects adjusted walking speed (solid black line) out of phase with speed ratio (when speed ratio increases, walking speed decreases). Data shown is a representative individual trial. *B*: this behavior is well described by a 2-process model fit (gray line) with a visual weighting parameter of 0.058 ± 0.001 and other model parameters identified from the step perturbations. This value suggests that vision accounts for ~5.8% of the sensory drive into prediction within our sine perturbation experiment. Although the fit was performed on normalized walking speed from individual trials, the shown data is the average over all trials. Values are means $\pm$ 95% CI.
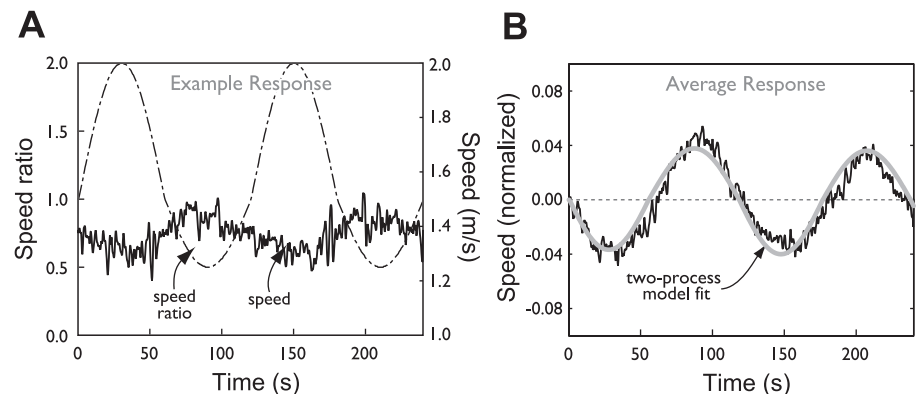
walking speed varied by 0.13 m/s across the range in speed ratios from 0.25 to 2.0. The two-process model (*Eq. 3*) explained 67% of the average subject behavior for the sine perturbations ($R^2 = 0.67$) (Fig. 5*B*).

DISCUSSION

In the present study we have demonstrated that vision is used for rapidly predicting and selecting preferred walking speeds by using virtual reality to invoke false perceptions of speed. In response to sudden perturbations of visually presented speed, we observed rapid adjustments to walking speed with response times of <2 s, or roughly over 3 steps. The directions of the rapid adjustments were consistent with an attempt by the subjects to return their visually presented speed back toward their preferred walking speed and occurred at the expense of actual walking speed. Subjects were induced to initially speed up or slow down entirely on the basis of the direction of the perturbation, and the speed changes were generally sustained over many steps. These effects are particularly striking when one considers that there was no physical perturbation: the subjects did not have to change speed to stay on the treadmill and would not have changed speed if they were to have disregarded the visual input or simply closed their eyes. The swiftness, direction, and persistent nature of the adjustments strongly indicate that vision is normally used to help select the preferred walking speed. Because people prefer walking speeds that minimize energetic cost of transport, these results suggest that vision is used to rapidly predict energetically optimal speeds.

We also observed a slow process that gradually corrected the effect of the visual perturbation and returned subjects back toward their originally preferred speed. Preferred walking speeds minimize energetic cost, raising the possibility that this slow process was acting to directly optimize energy use. Such a process would be expected to be relatively slow and only gradually converge to the optimal pattern because of the response times of the direct metabolic sensors as well as the need to iteratively adjust walking speed and reassess metabolic rate in a closed-loop process (Bellville et al. 1979; Coote et al. 1971; Kaufman and Hayes 2002; Smith et al. 2006; Snaterse et al. 2011). This is true even though the perturbations of speed ratio will affect the perceived cost of transport by manipulating subject estimates of walking speed (people must sense both metabolic rate and speed to estimate energy use per unit distance). For visual perturbations that only manipulate the gain between visual and actual walking speed, as in our experiment, the walking speed at which the perceived cost of transport is minimized remains unchanged (see APPENDIX). However, we cannot within our current experiment determine whether the observed slow adjustments are indeed acting as a separate optimization process or whether they result from a recalibration of self-motion perception, as may be the case when walking to a target under altered visual conditions (Durgin et al. 2005; Mohler et al. 2007c; Rieser et al. 1995). Many task goals inherent to walking require accurate knowledge of walking speed, and visual recalibration would be driven by a mismatch between visual and other sensory feedback for the purpose of best estimating speed. Future experiments could test for sensory reweighting by determining whether the gain on visual flow rate changes before and after sustained perturbations of speed ratio. Still, previous experiments examining adjustments to step frequency in response to sudden physical perturbations of treadmill speed also observed a slow process that cannot be attributed to sensory reweighting (Snaterse et al. 2011). Future experiments could also test for direct optimization by manipulating possible direct sensors of metabolic rate, such as the central and peripheral chemoreceptors, which are sensitive to the levels of oxygen and carbon dioxide in the blood (Bellville et al. 1979; Smith et al. 2006).

Indirect prediction represents a general mechanism for rapidly selecting gaits across a variety of contexts and situations. In addition to controlling speed, an effective predictive mechanism can help select other characteristics of gait that strongly affect energetic cost, such as step frequency (Doke et al. 2005; Elftman 1966; Gottschall and Kram 2005; Kuo 2001). It may also take into account environmental constraints, such as terrain, which affect the optimal gait patterns (Wickler et al. 2000). The speed at which gait transitions occur may also suggest such predictive control, given that people rapidly switch to a run before direct metabolic sensing could likely be useful (Hreljac 1993; Mercier et al. 1994; Thorstensson and Roberthson 1987). Therefore, perturbations that affect the energetic cost of gait, irrespective of whether they affect speed, step frequency, or another parameter, are likely to reveal fast and predictive dynamics. Our measured fast response time of 1.4 s for adjustments of walking speed after visual sensory perturbations is very consistent with the previously observed value of 1.4 s, found from adjustments of step frequency after sudden treadmill speed perturbations (Snaterse et al. 2011). Furthermore, a novel treadmill controller that adjusts speed as a function of measured step frequency was used to show that the fast adjustments in step frequency encode the relationship

between speed and frequency that minimizes energetic cost (Snaterse et al. 2011).

Under normal circumstances, predictive gait selection would not only rely on vision but also would integrate feedback from many different sensory modalities, such as proprioception and vestibular feedback, to best estimate speed. Proprioceptive feedback may in fact provide more direct walking speed information based on limb motions relative to a fixed support surface, whereas visually sensed speed must be indirectly surmised on the basis of the speed of object motion across the retina and an estimate of the distance of those objects to the person. The visual system must further distinguish between object and self-motion to estimate walking speed (Gibson 1958). The vestibular system is directly sensitive to self-motion but requires that the nervous system integrate acceleration signals from the otolith organs to estimate speed (Goldberg and Hudspeth 2000). To test the nature of the fast gait selection process, we used vision, rather than these other possibly more important sensory systems, largely because the visual pathways are the most readily perturbed. It should also be noted that the canceling effect between the two processes observed in our study would only occur in artificial situations with discordant sensory feedback. The sources of feedback that provide information about energetic cost and walking speed would all be congruent under normal situations and jointly contribute to induce gait changes consistent with energy optimization, albeit over different time scales.

We estimated the relative contribution of visual feedback to the selection of gait speed within our experimental paradigm as ~5.8% from sinusoidal perturbations and 10% from step perturbations. The similarity of these values, derived from different perturbations, provides a rough validation of our overall modeling approach. The differences may be attributed to variations in subjects' awareness of the perturbations and nonlinearities in the physiological system that senses and controls speed, as well as our data analysis methods (e.g., nonresponse trials were not included in the step analysis). These values compare well to the measure of 3.5% found from previous sinusoidal visual perturbations (based on reported data from Prokop et al. 1997). However, the small amplitudes should not be taken as evidence against the importance of vision in all contexts, since visual sensitivity is highly dependent on the reliability of the visual information relative to the other sensory pathways, and thus on the quality of the self-motion illusion created through virtual reality. Given the simplicity of the virtual environment provided in this experiment, subjects likely experienced changes in optic flow rate more so than perceived motion through a three-dimensional environment (Mohler et al. 2007c). By adding more realistic three-dimensional information to the visual feedback, the perturbation responses would likely increase over that produced by optic flow alone. We then suspect that whereas prediction likely relies on sensory feedback from many different sources, vision is likely used to a greater extent in normal walking than estimated here.

A major limitation of virtual reality is that subjects must implicitly trust the virtual environment and self-paced treadmill. Our protocol attempted to build this trust using a prior familiarization session, yet in a subset of step trials, subjects' lack of response suggested that the step perturbations were not always perceived as changes in the speed of self-motion.

However, the rejection responses still showed fast dynamics, indicating that visual prediction was first used and then quickly discarded. We interpreted the reduced sensitivity to visual perturbations as subjects either ignoring the smaller visual perturbations or learning to discard them after several trials. The numbers of these nonresponse and rejection trials (and again, the visual contribution measured from the step and sinusoidal perturbations) would likely be affected by subject immersion in the virtual environment as determined by subject factors such as concentration and immersive tendencies and by experiment factors such as realism of the virtual environment (Witmer and Singer 1998).

A second limitation is that we interpreted our results in terms of metabolic cost minimization, yet we never measured metabolic rate. This assumption is based on a long-standing body of evidence demonstrating that people freely select energetically optimal gait characteristics under controlled conditions (Donelan et al. 2001; Elftman 1966; Ralston 1958), including the speed that minimizes their metabolic energy cost per unit distance traveled (Bertram 2005; Bertram and Ruina 2001; Margaria 1938; Ralston 1958; Zarrugh et al. 1974). Indeed, we found the preferred walking speeds in our experiment to be very close to reported values that minimize the cost of transport (Browning and Kram 2005; Ralston 1958; Zarrugh et al. 1974). Of course, energy minimization must be considered against other important goals for walking, such as balancing to prevent injurious falls or walking to a target. These other goals, along with the environment, place constraints on acceptable walking patterns, whereas energy minimization appears to operate within these constraints to determine the preferred gait (Kuo and Donelan 2010; Sparrow and Newell 1998). However, the effects of these other constraints on preferred walking speed do not likely explain the results of this study. For example, the rapid adjustments do not resemble balance responses, because the visual perturbations induced speed changes in both directions that persisted for several minutes. Task goals such as arriving at a destination in a timely manner and environmental factors were also accounted for, since subjects walked down an endless hallway on a level treadmill.

A particular strength of our approach to studying gait speed selection is to consider not just the average response to a virtual reality perturbation but also the underlying dynamics of the processes involved. Previous work has shown that subjects adjust average walking speed after sustained changes in visually presented speed and in a direction opposite the change in perceived speed (De Smet et al. 2009; Mohler et al. 2007b). However, measures of average speed over a trial mask the amplitude and timing of the fast dynamics that produce this outcome as well as the slow process that eventually cancels it out. Previous sinusoidal visual perturbations have estimated the magnitude of the visual contribution to gait but have not been used to identify the timing of the processes involved (Lamontagne et al. 2007; Prokop et al. 1997). Our results are consistent with these previous findings but add significant insight by identifying the underlying processes that produce these behaviors, namely, a fast gait selection mechanism that responds to the altered visual stimuli and a slower process that gradually returns subjects back to steady state over several minutes. Gait speed selection is then similar to the control of heading in that visual flow rate is used rapidly for

online correction (Bruggeman et al. 2007). The outcome of this study also provides functional knowledge for using virtual reality to enhance rehabilitative gait training (Lamontagne et al. 2007) and suggests that reducing the visually perceived walking speed through a multiplicative gain will have a significant, albeit temporary, effect on increasing walking speed during a training session.

In summary, people use visual sensory information to rapidly predict and select preferred walking speeds as a likely complement to the direct sensing of metabolic rate. Gait optimization based on this direct sensing is more likely to refine gait over longer time scales. Energy minimization provides a central framework to understand these mechanisms underlying the control of walking and emphasizes the need for rapid control systems to optimize gait energetics. Although short-term walking behaviors are typically explained in terms of pattern generation and maintaining balance (Pearson and Gordon 2000), we find that the real-time control of walking also reflects the general goal of selecting preferred and energetically optimal gaits.

APPENDIX

Model of gait speed selection. This section presents the derivation of a model of gait speed selection in response to perturbations of visual flow rate through the speed ratio parameter. We hypothesize that there are two physiological processes, indirect prediction and direct optimization, that operate on different time scales and underlie the selection of preferred walking mechanics (Fig. 1). Practically, the indirect predictive process may be implemented by a feedback control system that attempts to reduce the error between the estimated speed v_{est}, based on sensory feedback, and the predicted optimal speed v_{pred}, given environmental and task limitations (Fig. A1A). Walking speed may be estimated from a weighted sum of the individual sensory components that provide feedback about the forward the velocity of the body. We represent this estimation as a sum of visual sensory information weighted by factor a and all other possible sources of velocity feedback weighted by factor $(1 - a)$, where a is between 0 and 1. In this model, speed ratio m is a multiplicative gain that acts on the actual walking speed v to give the visual speed, v_{vis} (*Eqs. 1* and *A1*). The direct optimization control process is generically represented as a black-box system that directly measures the metabolic consequences of walking at a given speed, combines estimated walking speed and measured metabolic rate to calculate cost of transport

Fig. A1. Models of gait speed selection. *A*: we hypothesize that there are 2 physiological processes, indirect prediction and direct optimization, that operate on different time scales and underlie the selection of preferred walking mechanics. Indirect prediction is represented by a feedback control system that minimizes the error between the predicted optimal speed v_{pred} and the estimated speed v_{est} based on weighted sensory feedback. The parameter a quantifies the relative weighting of visual speed information compared with speed information from other sensory sources. The speed ratio m is a multiplicative gain that acts on the actual walking speed v to give the visual speed v_{vis}. Direct optimization is represented as a black-box system that directly measures the metabolic consequences of walking speed, estimates COT based on speed and metabolic rate estimates, and adjusts speed to minimize the COT over time. These 2 control processes act on the body dynamics to produce changes in walking speed. *B*: reduced block diagram of gait speed selection based on linearization of the indirect sensors. The input into the system is change in speed ratio x applied at the preferred walking speed, and the output is the change in walking speed relative to the preferred walking speed, $v - v_{pref}$. *C*: linear model of gait speed selection for system identification, where s is the Laplace variable, $X(s)$ is the input (change in speed ratio), $Y(s)$ is the output (change in normalized walking speed), $G(s)$ represents the body dynamics, $P(s)$ represents the dynamics of prediction control that responds to the speed ratio perturbations, and $O(s)$ represents the dynamics of a direct optimization that rejects these adjustments.
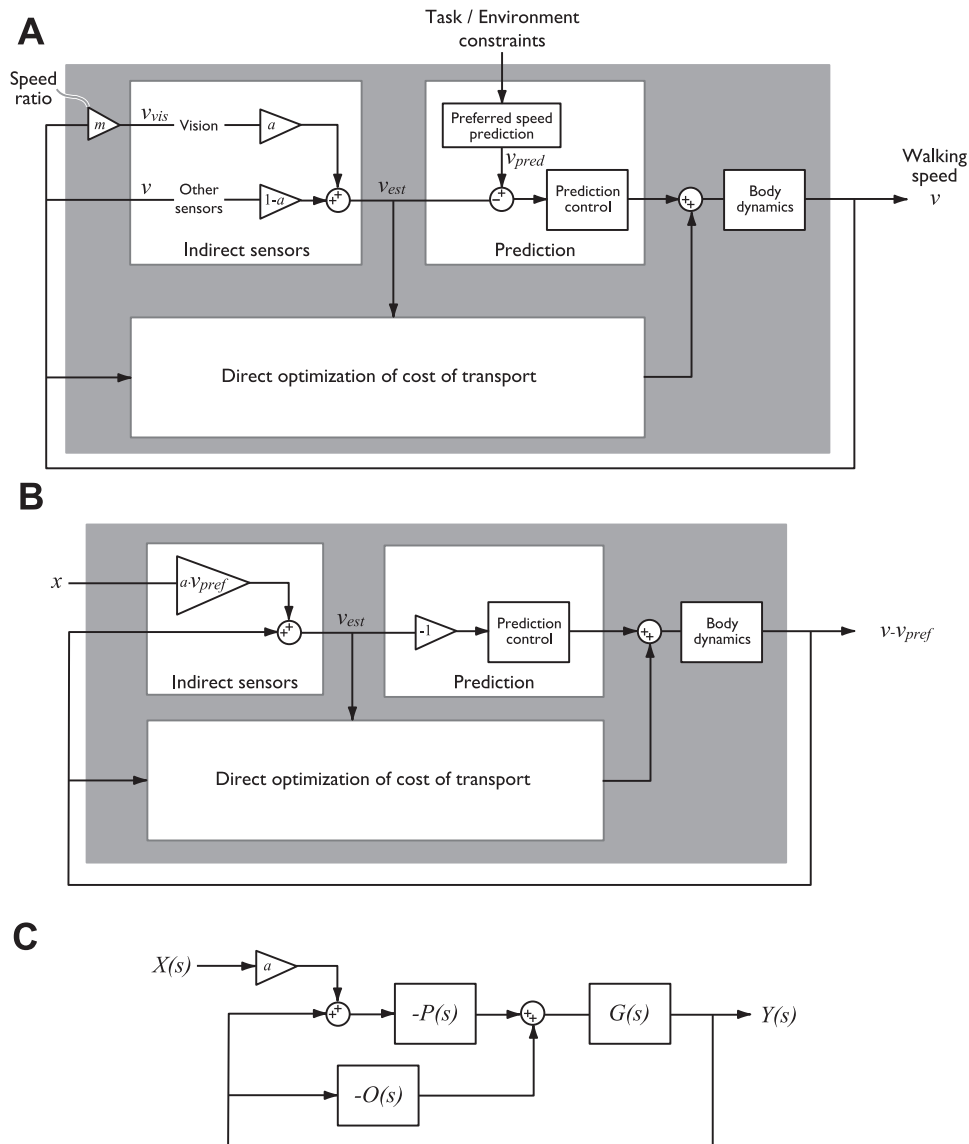
(COT), and attempts to minimize the cost of transport over time. These two control processes act on the body dynamics to produce changes in walking speed. To compare this model of gait speed selection with the measured input-output data particular to our experiment, we must first linearize the effect of the speed ratio input on walking speed adjustments. Careful normalization of the model inputs and outputs also greatly simplifies the model structure.

To treat speed ratio as a linear input into the system, we will linearize *Eq. A1* about the experimental control condition, where speed ratio is equal to the control value of 1 and the walking speed is equal to the preferred walking speed, v_{pref}. The full equation of the first-order approximation is shown in *Eq. A2* and simplified in *Eq. A3*.

$$v_{\mathrm{vis}}(m, v) = mv \qquad (A1)$$

$$v_{\mathrm{vis}}(m, v) \approx v_{\mathrm{vis}}(1, v_{\mathrm{pref}}) + \left.\frac{\partial v_{\mathrm{vis}}(m, v)}{\partial m}\right|_{\substack{m=1\\v=v_{\mathrm{pref}}}} (m - 1)$$
$$+ \left.\frac{\partial v_{\mathrm{vis}}(m, v)}{\partial v}\right|_{\substack{m=1\\v=v_{\mathrm{pref}}}} (v - v_{\mathrm{pref}}) \qquad (A2)$$

$$v_{\mathrm{vis}}(m, v) \approx v_{\mathrm{pref}} m + v - v_{\mathrm{pref}} \qquad (A3)$$

We can now treat the speed ratio m as an additive input that alters visual speed. For a speed ratio equal to 1, the visual speed is equal to the walking speed. To analyze the effect of perturbations of speed ratio on walking speed dynamics, we will define the input into the system x as

$$x = m - 1, \qquad (A4)$$

where x is then the change in speed ratio relative to the control value of 1. Substituting *Eq. A4* into *Eq. A3*, we arrive at a simplified linear model of the virtual manipulations of vision (*Eq. A5*):

$$v_{\mathrm{vis}}(x, v) \approx v_{\mathrm{pref}} x + v \qquad (A5)$$

Given this simplification, the model of speed estimation, which sums weighted sensory components, reduces to

$$v_{\mathrm{est}}(x, v) = a v_{\mathrm{vis}} + (1 - a)v \approx a v_{\mathrm{pref}} x + v \qquad (A6)$$

where the other sources of velocity feedback are combined and assumed to provide direct information about walking speed v. This simplified model is reflected in an updated block diagram of gait speed selection, where the input into the system x is change in speed ratio applied at the preferred walking speed and the output $v - v_{\mathrm{pref}}$ is the change in walking speed relative to the preferred walking speed (Fig. A1*B*). Note that the predicted optimal speed input v_{pred} from Fig. A1*A* is no longer considered in this analysis because we are modeling the effect of changes in speed ratio on changes in walking speed, and v_{pred} is assumed to be fixed given constant task and environmental conditions during the experiment.

To compare walking speed adjustments across subjects and to further simplify the equations of our model, we define a normalized output of the system y as

$$y = \frac{v - v_{\mathrm{pref}}}{v_{\mathrm{pref}}} \qquad (A7)$$

where y represents changes in the normalized walking speed due to input perturbations of speed ratio.

We are now ready to compose a linear model to represent the input-output dynamics of normalized walking speed adjustments in response to perturbations of speed ratio. Indirect prediction control is approximated as a linear transfer function that rejects changes in the estimated speed away from the preferred speed. The direct optimization control process is approximated by a linear transfer function that rejects adjustments of walking speed that diverge from the preferred and energetically optimal speed. Although sensing walking speed is necessary to estimate the COT, we neglect this as an input into the optimization process because perturbations of speed ratio are not

expected to alter the speed that minimizes the estimated COT (see APPENDIX, *Perception of minimum cost of transport*). These two control processes act in parallel as inputs into the body dynamics. The body dynamics are approximated as a linear transfer function that maps forces related to control to changes in walking speed. The final linear representation of our model used for system identification is given in Fig. A1*C* and *Eq. A8* as

$$Y(s) = \left(\frac{-a \cdot G(s) \cdot P(s)}{1 + G(s) \cdot P(s) + G(s) \cdot O(s)} \right) X(s), \qquad (A8)$$

where s is the Laplace variable, $X(s)$ is the input (change in speed ratio), $Y(s)$ is the output (change in normalized walking speed), $G(s)$ represents the body dynamics, $P(s)$ represents the dynamics of indirect prediction control that responds to the speed ratio perturbations, and $O(s)$ represents the dynamics of a direct optimization control process that rejects these adjustments.

We chose functions for the processes to produce the hypothesized rapid response to visual perturbations, and its gradual rejection, with the fewest number of parameters, where

$$G(s) \cdot P(s) = \frac{1}{\tau_{\mathrm{f}} s}, \quad G(s) \cdot O(s) = \frac{1}{\tau_s s^2},$$
$$Y(s) = \left(\frac{-a \tau_s s}{\tau_{\mathrm{f}} \tau_s s^2 + \tau_s s + \tau_{\mathrm{f}}} \right) X(s). \qquad (A9)$$

Here, $G(s)$ and $P(s)$ are combined to yield a fast process that quickly adjusts speed in response to the input, and $G(s)$ and $O(s)$ are combined to yield a slow process that slowly adjusts speed to reject these changes away from the optimal speed. The parameters τ_{f} and τ_s represent timing parameters for the fast and slow processes and have units of seconds and seconds squared, respectively.

A possible implementation of the individual processes $G(s)$, $P(s)$, and $O(s)$ that would produce the model in *Eq. A9* is as follows, where

$$G(s) = \frac{1}{Ms}, \quad P(s) = K_f, \quad O(s) = \frac{K_s}{s} \qquad (A10)$$

Here, M is the body mass and $G(s)$ represents a very simplified musculoskeletal model that integrates muscle force inputs to produce a velocity output. Indirect prediction $P(s)$ and direct optimization $O(s)$ then take the form of a proportional integral (PI) controller, where the fast predictions occur from the proportional gain K_{f} and the slower corrections come from the integral term K_s. This PI controller form is equivalent to *Eq. A9* for $\tau_{\mathrm{f}} = M/K_{\mathrm{f}}$ and $\tau_s = M/K_s$. Although this particular implementation provides a useful conceptualization of how the processes might act to control speed, it does require additional assumptions about the nature of the individual processes [e.g., for $G(s)$, the faster dynamics of the motor control system are approximated as negligible]. The more general form (*Eq. A9*) is therefore used for system identification to avoid unnecessary assumptions about the individual processes.

Perception of minimum cost of transport. This section presents analysis of the effect of visual perturbations on the perception of energy expenditure during walking. If an optimization process were to minimize the metabolic COT, defined as the metabolic rate per unit of walking speed, this process would require simultaneous sensing of both speed and metabolic rate. Therefore, visual perturbations that create false estimations of walking speed will alter estimates of the COT. Here we formulate the effect of these perturbations on the estimated COT to predict how the visual perturbations in our experimental paradigm would affect optimizations of walking speed.

Previous experiments have empirically found a quadratic relationship between walking speed v and metabolic rate, $\dot{E}_{\mathrm{met}}$ (*Eq. A11*) (Ralston 1958; Zarrugh et al. 1974):

$$\dot{E}_{\text{met}} = a_1 + a_2 v^2. \qquad (A11)$$

The regression coefficients a_1 and a_2 are determined from experimental data. The cost of transport, E_{COT}, is given by dividing *Eq. A11* by walking speed (*Eq. A12*):

$$E_{\text{COT}} = a_1/v + a_2 v. \qquad (A12)$$

The speed that minimizes COT can be found by taking the derivative of *Eq. A12* with respect to v, equating the derivative to zero, and solving for v. The minimum then occurs at a speed of $\sqrt{a_1/a_2}$, which is equivalent to 1.33 m/s based on previously determined values for a_1 and a_2 (Zarrugh et al. 1974).

We may similarly calculate an estimated COT, E_{est}, by dividing *Eq. A11* by estimated walking speed, v_{est}, which is likely obtained from visual, proprioceptive, and other sensory feedback (*Eq. A13*):

$$E_{\text{est}} = \dot{E}_{\text{met}}/v_{\text{est}} = a_1/v_{\text{est}} + \left(a_2 v^2\right)/v_{\text{est}}. \qquad (A13)$$

To simplify the analysis, we first assume that the speed estimate is made entirely from visual speed, v_{vis}. Let estimated speed then be a function of actual walking speed and possible virtual manipulations of the visual flow rate (*Eq. A14*):

$$v_{\text{est}} = v_{\text{vis}} = mv + b. \qquad (A14)$$

Here, m is a gain on visual flow rate equivalent to the speed ratio variable in the experiment and b is an offset in flow rate. Estimated COT can then be expressed as a function of the actual walking speed (*Eq. A15*):

$$E_{\text{est}} = a_1/\left(mv + b\right) + \left(a_2 v^2\right)/\left(mv + b\right). \qquad (A15)$$

Visual speed perturbations will then change the shape of the estimated COT curve. We can calculate the speed that minimizes the estimated COT by again taking the derivative of this function and equating to zero.

For visual perturbations that only manipulate the visual gain ($b = 0$), as we have done in the present experiment, the minimum estimated COT occurs at a speed of $\sqrt{a_1/a_2}$. Importantly, the optimal speed that minimizes estimated COT is the same as the optimal speed based on the actual minimum COT. This prediction remains true even when considering that other senses such as proprioception would also be used to estimate speed (analysis not shown).

For visual perturbations that only manipulate the visual offset ($m = 0$), the minimum estimated COT is occurs at a speed of $\sqrt{a_2^2 b^2 + a_2 a_1}/a_2 - b$. Visual offset perturbations then result in an estimated optimal speed that differs from the actual optimal speed. When the visual offset is positive, the optimal speed is falsely estimated as lower than the actual optimal speed. This result may then explain why people slow down when walking on a moving walkway at the airport, which has been predicted from a similar analysis (Srinivasan 2009).

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DISCLOSURES

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AUTHOR CONTRIBUTIONS

Author contributions: S.M.O. and J.M.D. conception and design of research; S.M.O. performed experiments; S.M.O. and J.M.D. analyzed data; S.M.O. and J.M.D. interpreted results of experiments; S.M.O. prepared figures; S.M.O. drafted manuscript; S.M.O. and J.M.D. edited and revised manuscript; S.M.O. and J.M.D. approved final version of manuscript.

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