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RESEARCH ARTICLE | *Control of Movement*

Is natural variability in gait sufficient to initiate spontaneous energy optimization in human walking?

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Wong JD, Selinger JC, Donelan JM. Is natural variability in gait sufficient to initiate spontaneous energy optimization in human walking? *J Neurophysiol* 121: 1848–1855, 2019. First published March 13, 2019; doi:10.1152/jn.00417.2018.—In new walking contexts, the nervous system can adapt preferred gaits to minimize energetic cost. During treadmill walking, this optimization is not usually spontaneous but instead requires experience with the new energetic cost landscape. Experimenters can provide subjects with the needed experience by prescribing new gaits or instructing them to explore new gaits. Yet in familiar walking contexts, people naturally prefer energetically optimal gaits: the nervous system can optimize cost without an experimenter's guidance. Here we test the hypothesis that the natural gait variability of overground walking provides the nervous system with sufficient experience with new cost landscapes to initiate spontaneous minimization of energetic cost. We had subjects walk over paths of varying terrain while wearing knee exoskeletons that penalized walking as a function of step frequency. The exoskeletons created cost landscapes with minima that were, on average, 8% lower than the energetic cost at the initially preferred gaits and achieved at walking speeds and step frequencies that were 4% lower than the initially preferred values. We found that our overground walking trials amplified gait variability by 3.7-fold compared with treadmill walking, resulting in subjects gaining greater experience with new cost landscapes, including frequent experience with gaits at the new energetic minima. However, after 20 min and 2.0 km of walking in the new cost landscapes, we observed no consistent optimization of gait, suggesting that natural gait variability during overground walking is not always sufficient to initiate energetic optimization over the time periods and distances tested in this study.

NEW & NOTEWORTHY While the nervous system can continuously optimize gait to minimize energetic cost, what initiates this optimization process during every day walking is unknown. Here we tested the hypothesis that the nervous system leverages the natural variability in gait experienced during overground walking to converge on new energetically optimal gaits created using exoskeletons. Contrary to our hypothesis, we found that participants did not adapt toward optimal gaits: natural variability is not always sufficient to initiate spontaneous energy optimization.

energy optimization; gait; locomotion; motor learning; variability

INTRODUCTION

Our nervous systems have converged on movements that minimize metabolic energetic cost (Atzler and Herbst 1927; Bertram and Ruina 2001; Donelan et al. 2001; Ralston 1958; Minetti and Alexander 1997; Zarrugh et al. 1974). We refer to the process by which people adapt behavior toward energetically optimal behavior, without necessarily converging to the global optimum, as "gait optimization." While this movement optimization may occur over developmental and evolutionary time scales, we recently found that the nervous system can also optimize for energetic cost in real-time (Selinger et al. 2015). In these experiments, subjects walked while wearing exoskeletons controlled to reshape the normal relationship between step frequency and energetic cost. (We refer to relationships between behavior and energetic cost as "cost landscapes.") These reshaped cost landscapes shifted the energetically optimal step frequency away from the initially preferred, and previously optimal, step frequency. By the end of these experiments, subjects converged to walk at the new step frequency that minimized energetic cost, gaining an energetic savings of as little as 4% of the total cost of walking. The nervous system can therefore be frugal when adapting movements to optimize for energetic cost.

The nervous system may require experience with new cost landscapes to initiate energy optimization. When the exoskeletons were first engaged to reshape the cost landscapes in the above experiments, subjects did not immediately initiate energy optimization. Instead, optimization occurred while subjects self-explored a range of step frequencies and while a metronome guided subjects through a similar range of frequencies. This 15-min protocol may have initiated optimization because it increased the experience with the new cost landscape, which is limited by the low natural gait variability during treadmill walking. Under steady-state walking the standard deviation of step frequency is ~1.5% of the preferred frequency (Danion et al. 1997; Pagliara et al. 2014; Selinger et al. 2015). The exoskeletons were controlled such that each 1% shift in step frequency produced between 1 and 2% reductions in energetic cost. Therefore, most steps that people took during steady-state walking had small energetic consequences. The additional experience provided within our experimental protocol may have been successful in initiating optimization because it supplemented people's natural variability with greater exploration of the cost landscape.

However, people naturally prefer optimal gaits, suggesting that some mechanism other than experimenter guidance allows the nervous system to learn relationships between behavior and

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energetic cost. Perhaps the simplest hypothesized mechanism to learn this relationship in gait and, in motor learning more generally, is that the nervous system uses variability in behavior to learn how changes in motor output produce changes in cost (Tumer and Brainard 2007; Wu et al. 2014). This requires that the nervous system can quantify both the behavioral variability and its sensory consequences. This is physiologically plausible as the nervous system can estimate variability through a combination of prediction via efference copy and feedback from sensory receptors (Blakemore et al. 1998; Wolpert and Flanagan 2001). In addition, the nervous system may estimate the energetic consequences using direct metabolic sensors (Amann 2012; Amann et al. 2010), or their proxies (Hubbuch et al. 2015). Behavioral variability under this hypothesis is thus not merely noise that comes from incomplete learning or imperfect control but rather a mechanism for the nervous system to experience new costs that are associated with novel contexts or environments. The idea of variability for motor exploration is simple but surprisingly powerful. Indeed, many modern learning algorithms learn to operate within their environments using motor variability to sample different behaviors and their costs. Such approaches have helped produce state-of-the-art performance in discrete-time and perfect information games such as the board game Go, continuous-control during video games such as League of Legends, and promising results in simulated and physical robots (Gu et al. 2016; Lillicrap et al. 2015; Mnih et al. 2016). While to our knowledge motor variability has not been explored in the context of energy optimization, there is evidence that biological systems structure behavioral variability during motor learning in other domains such as the adaptation of bird song and human skill acquisition (Tumer and Brainard 2007; Wu et al. 2014). Song-to-song variability in finches has been shown to represent meaningful motor exploration rather than merely the result of noisy movement execution, and people with greater reaching variability at baseline have been observed to have faster learning rates.

Here we test the hypothesis that the nervous system uses the natural variability in overground walking to initiate optimization of energetic cost. To test this hypothesis, subjects wore a custom-built portable control system that measured overground speed and step frequency and commanded frequency-dependent resistive torques to knee-mounted exoskeletons. We used the same relationship between step frequency and resistive torque from our previous study to reshape the relationship between energetic cost and gait. We measured how subjects preferred to walk under this new cost landscape during a paradigm that directed subjects to walk along predefined paths that traversed terrain with varying grades and curvatures. We designed these paths to increase the range of step frequencies and speeds exhibited by subjects and thus provide them with experience with the new relationship between gait and energetic cost. To determine changes to preferred speed and step frequency, subjects periodically returned to a probe section of the path that had zero curvature and zero grade. Changes to preferred gait toward the energetically optimal gait would support the hypothesis that natural variability in overground walking provides sufficient experience for the nervous system to initiate energy optimization.

METHODS

Ten subjects (means ± SD age: 21 ± 4.3; height: 171 ± 10 cm; and mass: 66.6 ± 9.6 kg) participated in the study. All were healthy adults with no known history of cardiovascular, musculoskeletal, neurological, or respiratory impairments. Subjects gave written informed consent before participation. The Simon Fraser University Research Ethics Board approved all procedures.

During our experiments, subjects wore a 1.1-kg exoskeleton on each leg and a 4.5-kg backpack containing our speed-sensing, control, and power electronics (Fig. 1*A*). They also wore gyroscopes placed on both shoes, secured with clips and tape. A backpack-mounted microcontroller (Arduino Due; Arduino) sampled these gyroscope angular velocity signals (iNemo LSM9DS1) at 500 Hz and then digitally filtered them (one-directional, first-order, low-pass, 4 Hz cut-off,

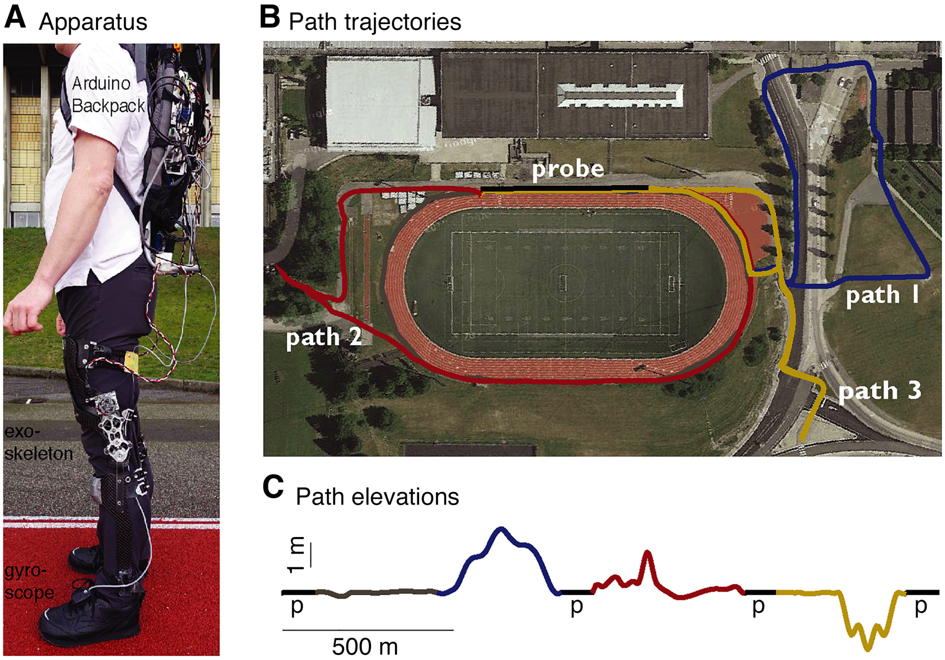

Fig. 1. *A*: apparatus. Subjects wore knee exoskeletons, which applied a controllable resistive torque at the knee. A microcontroller housed within a lightweight (4.5 kg) backpack commanded resistive torque to the knee exoskeletons and performed data logging. Subjects wore gyroscopes fixed to their shoes from which foot contact was detected and step frequency was computed. Subjects also wore a global positioning system antenna (Racelogic) affixed to a hat (not shown). *B*: protocol. Subjects began the adaptation protocol walking one lap of the track (gray) and then proceeded through paths 1 (blue), 2 (red), and 3 (yellow). Each path and track section finished with the probe section (black), which was a flat and straight fixed portion of the protocol. *C*: elevation changes throughout the protocol. Path sections are denoted using colors matching *B*.

Butterworth filter). Algorithms running on the microcontroller detected a foot contact event when a foot's angular velocity decreased below 0.9 rad/s and then computed step frequency as the inverse of the period between left and right foot contact events. The microcontroller logged this step frequency to an SD card for subsequent analysis. Next, the microcontroller applied a three-step median filter to the step frequency to smooth the signal used for torque commands, in a manner similar to Selinger et al. (2015), and then commanded resistive torques to the exoskeleton as a function of this filtered step frequency. It updated the commanded torque with each new walking step. The particular control function used in this study applied the greatest resistance to knee motion (12 Nm) at high step frequencies (greater than +10% from the initially preferred step frequency), the lowest resistance (2 Nm) at low step frequencies (less than −15% of the initially preferred step frequency), and varied torque linearly between these two extreme step frequencies. A more detailed description of the mechanics and control of our exoskeletons can be found in Selinger et al. (2015). A high-performance global positioning system device measured real-time walking speed (VBOX Speed Sensor; Racelogic, Buckingham, UK; 10-Hz sampling frequency; 43-ms time delay). It is quite accurate, with an average and root mean square error of −0.2 and 2%, respectively (Pagliara et al. 2014). The microcontroller averaged global positioning system speed between contact events to compute an average speed per step and logged these data to the SD card.

Our experimental protocol began by outfitting subjects with the exoskeletons, gyroscopes, and backpack (Fig. 1 and Table 1). To familiarize them with the apparatus and conditions, subjects next completed two laps around an outdoor athletic track. They walked around the outside lap, which was 450 m in length and the two laps took between 10 and 12 min. During this time, the exoskeleton controller did not engage the control function. Next, subjects completed one additional lap while the exoskeleton applied a peak torque during the gait cycle of 7.2 Nm that was independent of step frequency (Selinger et al. 2015; see source data in ENDNOTE). We quantified the "initial preferred step frequency" and "initial preferred speed" as the average values during the last 75 m of this lap. We chose to apply this constant torque while quantifying the initially preferred values, as it is also the resistance that the controller would apply when subjects walked at their initial preferred frequency and speed during the subsequent experience phase of the protocol.

The experience phase of the protocol began when we engaged the penalize-high control function. First, to determine if increased variability experienced during overground but level walking is sufficient to initiate gait optimization, subjects completed another 450-m track lap (Fig. 1*B* gray). We refer to this subphase of the experience protocol as "track" walking. Next, to determine if still greater variability would initiate gait optimization, we asked subjects to walk along three paths in succession, each of which was ~500 m in length (Fig. 1*B*, blue, red and white in order). We refer to this sub-phase as "path" walking. Paths varied in terms of elevation changes and heading changes in an effort to provide variability beyond track walking (Fig. 1*C*). Each of the three paths finished with the same 70-m section that we termed the "probe" section of the protocol (Fig. 1*B*, black). This level and straight section of the athletic track was walked four times throughout the experience phase and allowed us to determine any changes to preferred step frequency and speed that were not due to variations in terrain. We quantified the "final preferred step frequency" and "final preferred speed" as the average values during the last probe. The experimenter explained each path's trajectory to the subject immediately before they walked it on their own. Paths were delineated using small flags on stakes and visual landmarks. At the beginning of each path description the experimenter gave the same instructions: "This section of the protocol is approximately 500 m. Please walk in whatever way you feel [*sic*]." The experimenter did not follow or lead the subject during any of the walking sections and instead met the subject each time they returned to the end of the probe section. In total, the experience phase totaled 2,000 m of walking, which subjects completed in ~20 min.

Table 1. *The distances for each portion of the experience phase of the experiment protocol*

Event	Distance, m
Baseline	900
Baseline-constant torque	450
Track	450
Path 1	520
Path 2	505
Path 3	490

We next determined whether the exoskeleton control function created an energetic minimum away from the initial preferred gait. To accomplish this, subjects completed a second experimental session that took place indoors on an instrumented treadmill (FIT; Bertec). It was completed on a different day to prevent subject fatigue, but within 1 wk of the outdoor experiments. We estimated metabolic cost by measuring inspired and expired gases to perform indirect calorimetry (VMax Encore Metabolic Cart; ViaSys (Brockway 1987)). We kept the conditions of the metabolic measurement day as close as possible to the conditions of the adaptation day. Subjects wore the same shoes on both days and fasted for 4 h and from strenuous exercise for at least 24 h. The time of day was also approximately matched such that metabolic measures were taken within 2 h of the time of day of the overground adaptation experiment. These precautions would help reduce, but not eliminate, the variation of cost landscapes between experimental sessions. Each trial was 5 min in duration: we allowed 3 min for subjects to reach steady state and then averaged metabolic power for the final 2 min of each trial (Browning and Kram 2005). We then calculated cost of transport, which is our measure of energetic cost in this experiment, as the metabolic power (in Watts) divided by walking speed, and normalized for body weight (in Newtons). We performed these experiments on a treadmill (again donning the exoskeleton and backpack), rather than overground, because the treadmill allowed us to precisely control the walking speed. We used a metronome to command the desired step frequencies to the subjects and asked that they synchronized their step frequency to the metronome beat. We then confirmed that they accurately matched the desired step frequencies using step frequency measures from the instrumented treadmill (means ± SD difference between metronome and actual step frequency: 0.24 ± 0.73 beats/min).

One approach to characterize the shape of the new cost landscape is to measure metabolic cost at an equally spaced two-dimensional grid of speed and step frequency values, encompassing the range of gaits experienced by each subject. Because we did not know a priori the gait about which subjects would finally adapt, and because such a systematic measurement would require subjects to walk for a long time (at least several hours), we took a different approach and measured metabolic cost locally around two step frequency/speed combinations: the subject's initial preferred speed and step frequency and final preferred speed and step frequency. This allowed us to determine if subjects made changes to preferred gait toward a local minimum. Subjects completed, in a randomized order, 10 trials of 10 different speed and step frequency combinations. One of these combinations was the subject's initial preferred speed and initial preferred step frequency. We bracketed the initial preferred gait with four additional combinations of step frequency and speed where one of these values was held higher, or lower, by 5% of the preferred value. Similarly, we measured metabolic cost at the final preferred speed and step frequency and bracketed that gait with combinations of speed and frequency that were ±5% of the final preferred values. While no change in gait between initial and final preferred would therefore mean metabolic cost would be measured twice at identical speed/step frequency combinations, the majority of subjects showed some deviation in preferred gait (see RESULTS and Fig. 5). For two subjects, we mistakenly measured metabolic cost at speeds and frequencies different than their final preferred. For the final preferred speed and step frequency values, we used −17.9 and +2.6% for *subject 2* and −9.6 and −4.4% for *subject 8*. We measured metabolic cost at these combinations, as well as ±5% of these values. Because in both cases the subjects' true final preferred speeds and step frequencies occurred within ±5% of initial preferred, we have performed linear interpolation using the data collected about initial preferred to compute the metabolic cost at these two subjects' final preferred speeds and step frequencies. We have included the metabolic data collected at these slow speeds in our individual data plots (see Fig. 5) and in our averaged bar plots of minimum cost (see Fig. 2), since these data still provide information about metabolic cost changes for different gaits. We also verified that our major conclusions are unaffected by the removal of these two subjects from our analysis.

To test whether variability was greater during track and path walking than on the treadmill, we quantified the amount of variability subjects made in speed and step frequency using data from individual steps during the track and path sections of the protocol. We measured variability as the standard deviation of speed and step frequency normalized to each subject's initial preferred values, giving the coefficient of variation of speed and step frequency. We computed the percentage of the coefficient of variation between overground (track and path) and treadmill walking. To determine how large the variability was relative to the energetic gradient, we compared the coefficient of variation in speed and step frequency to the change in speed and step frequency needed by subjects to shift their gait to their own local energetic minimum. We performed one-tailed, paired *t*-tests to determine if the metabolic energetic cost measured at the subject's local minimum was reliably higher than that measured at the subject's initial baseline and at the subject's final preferred gait. We performed one-tailed, paired *t*-tests to determine if the speeds and step frequencies at subjects' final preferred were lower than both the energetic minimum (in both speed and step frequency) and initial preferred. By design we created the energetic minimum to occur at lower step frequencies (Selinger et al. 2015) and predict this to also require decreases in speed (Atzler and Herbst 1927; Kuo 2001; Ralston 1958; Zarrugh et al. 1974).

RESULTS

Walking in the exoskeletons resulted in an energetic minimum away from the initial preferred step frequency and speed. Across subjects, the minimum measured energetic cost of transport occurred at a lower step frequency relative to the initial preferred frequency (–3.61 ± 4.07%, means ± SD; P = 0.011, paired *t*-test; Fig. 2*A*). Although the exoskeleton controlled resistance only as a function of step frequency, the minimum measured energetic cost also occurred at a lower speed relative to the initial preferred speed (−4.21 ± 6.11%; P = 0.024, paired *t*-test; Fig. 2*B*). We anticipated this finding because the optimal step frequency increases with walking speed (Atzler and Herbst 1927; Bertram and Ruina 2001; Kuo 2001; Molen et al. 1972; Ralston 1958; Zarrugh et al. 1974), and as a consequence, our control function disproportionately penalized the optimal step frequencies at the faster speeds. The metabolic cost at the combination of speed and step frequency that had the lowest measured cost was 5.38 ± 1.01 $\mathrm{J \cdot m^{-1} \cdot kg^{-1}}$ on average, while the energetic cost at the initial preferred step frequency and speed was 5.83 ± 0.92 $\mathrm{J \cdot m^{-1} \cdot kg^{-1}}$. Therefore, walking at the optimal combination of step frequency and speed that we measured resulted in a reduced metabolic cost of 8.0 ± 4.7% when compared with the cost at the initial preferred step frequency and speed (P = 3.5e-4, paired one-tailed *t*-test; Fig. 2*C*).

During the overground walking protocol, our subjects exhibited large variability in their selected step frequencies and speeds when compared with treadmill walking (Fig. 3). During track walking, the coefficient of variation in step frequency was 5.09 ± 1.28%, (SD normalized for the initial preferred step frequency). This was 3.0 times greater than treadmill walking, where the variability in step frequency is only 1.67 ± 0.35%. The step frequency variability during path walking was 6.14 ± 1.01%, representing a 3.7-fold increase over treadmill walking. While we did not quantify speed variability during treadmill walking, others have estimated it at 2.58 ± 1.06% (Sloot et al. 2013). In our experiments, the variability in speed during track and path walking were 6.70 ± 0.92 and 10.55 ± 1.67%, respectively. These are 2.6 and 4.1 times the speed variability estimated for treadmill walking.

With this variability in step frequency and speed, subjects gained experience with a greater range of speeds and step frequencies in their new cost landscape, including with lower costs gaits. This is illustrated in both Figs. 3 and 4, where the energetically optimal combination of step frequency and speed in the new cost landscape falls well within the distribution of frequencies and speeds exhibited by our subjects over the course of the experience protocol. Indeed, the ~4% shifts in preferred step frequency and speeds required to optimize cost

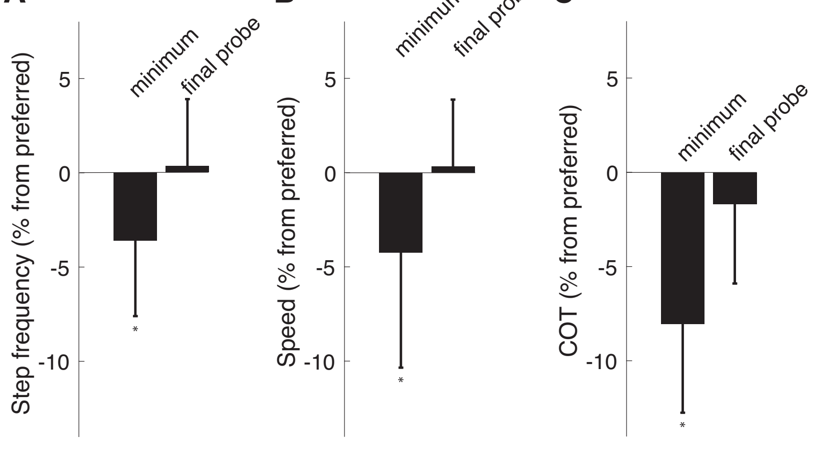

Fig. 2. *A*: the step frequency at the measured energetic minimum and at the final preferred gait (final probe). *B*: the speed at the measured energetic and final preferred gaits. *C*: the energetic cost at the measured energetic minimum, and final preferred gait. Values are normalized with respect to initial preferred, meaning that negative values reflect cost savings compared with initial preferred gait. The control function created an energetic minimum that had measurable savings relative to initial preferred walking and that occurred for speeds and step frequencies different than initial preferred. COT, cost of transport. *A–C*, *right*: the energetic cost, speed, and step frequency of the final adapted gait demonstrated by subjects. Bars represent 1 SD. *Significant differences from initial preferred values.

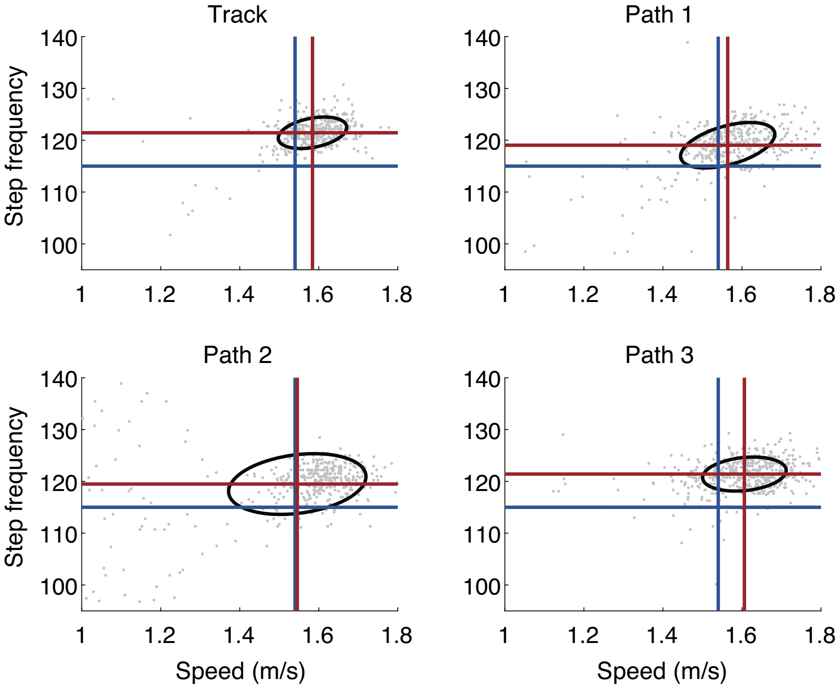

Fig. 3. Step-to-step variability in speed and step frequency: representative subject. Each dot represents a single step taken from a representative subject during the complete adaptation protocol, divided into track, path 1, path 2, and path 3. Red ellipses depict 1 SD in the 2 variables; the orientation of the ellipse depicts the degree to which these 2 variables covary. The red lines intersect at the mean speed and step frequency for the given trial, while the blue lines intersect at the energetic minimum for the example subject.

is less than a single standard deviation away from the initial preferred values. Over the course of the experiment, subjects took on average 451 (± 319) steps within 2% of minimum, and on average ~260 of those occurred on level terrain.

Despite the cost savings when adopting different step frequencies and speeds, and the considerable experience with walking at these lower cost gaits, subjects did not adapt their preferred step frequency or speed. The final preferred step frequency, 121.9 ± 5.4 steps/min, was not different from the initial preferred step frequency, 121.7 ± 5.5 steps/min (P = 0.590, one-tailed t-test; Fig. 2*A*). Similarly, the final preferred speed, 1.61 ± 0.08 m/s, was not different from the initial preferred speed, 1.60 ± 0.05 m/s ($P = 0.594$, one-tailed t-test; Fig. 2*B*). The change in metabolic cost of transport at subjects' final preferred was not reliably different from 0 (mean −1.69 ± 4.20%; $P > 0.05$, paired one-tailed t-test; Fig. 2*C*).

Figure 5 depicts the step frequency and speed for each subject at both the final preferred gait, and the gait with the minimum measured energetic cost. For most subjects, reducing their step frequency or speed from their final preferred value by ~1% would have gained them about a 1% reduction in cost. Moreover, the measured minimum cost combination of speed

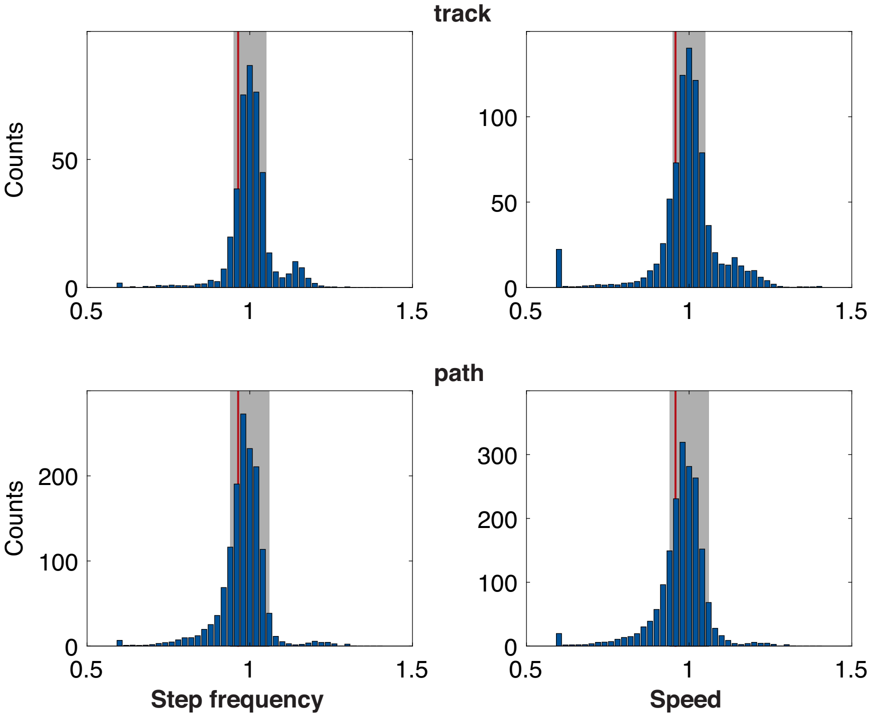

Fig. 4. Histogram of the number of steps taken at various speeds and step frequencies during the Track and Path parts of the adaptation protocol, averaged across subjects. Both speed and step frequency are normalized to initial preferred speed and step frequency. The gray bar depicts ± 1 SD. The red line denotes the speed and step frequency that on average minimized energetic cost across subjects.

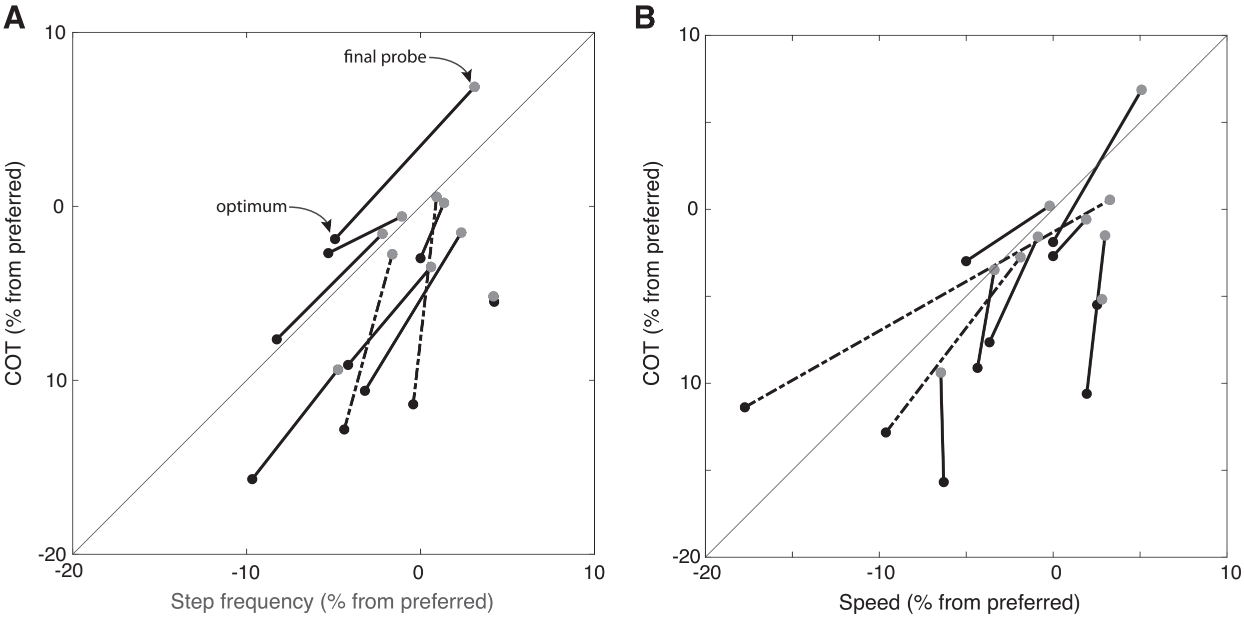

Fig. 5. Individual subject data: cost of transport, measured at both the final preferred (final probe) and energetically optimal gaits. *A*: the gray dots represent each subject's step frequency (*x*-axis) and cost of transport (*y*-axis) at the final probe. The black dots represent the step frequency and cost of transport (COT) at the energetic minimum. The black lines connect data from each subject and give a visual depiction of the slope that relates changes in step frequency to changes in metabolic cost of transport. *B*: as in *A*, but the *x*-axis is walking speed. The dotted lines reflect 2 subjects who had their second set of metabolic measurements mistakenly taken at lower speeds and step frequencies, and for whom final preferred metabolic cost was computed via linear interpolation (see METHODS).

and step frequency was nearby the final preferred combination and would have resulted in significant cost savings relative to the final preferred step frequency and speed (6.42 ± 3.7%; $P = 3.8e-4$). However, subjects had not learned to prefer the optimal speed and step frequency by the protocol's end. While our experimental paradigm seems sufficient to test our hypothesis, the results do not support it: the natural variability experienced in our overground walking trials was not sufficient experience for the nervous system to initiate optimization of energetic cost.

DISCUSSION

Here we tested the hypothesis that natural gait variability provides the nervous system with sufficient experience for it to spontaneously initiate optimization of energetic cost. To accomplish this, we used knee exoskeletons that shift the energetically optimal gait away from the initial preferred gait to lower speeds and step frequencies. We then gave subjects experience with their new cost landscape, during overground walking on variable terrain, providing them experience with a variety of gaits, including the energy optimal gait. However, subjects did not adapt their step frequency or speed by even a modest amount. This suggests that natural gait variability provided is not sufficient for the nervous system to spontaneously initiate energetic optimization.

We would have expected the cost savings to be sufficient. The cost savings here were about the same size as those in our previous experiment (~8%), yet those subjects reliably adapted their gait to minimize cost (Selinger et al. 2015). The location of the new optimal gait was about the same change in step frequency from the initial preferred gait in both experiments, and perhaps closer in our new experiment, indicating the gradient in cost about the initial preferred gait was about the same (~1–2% savings per 1% change in step frequency or speed). Several studies have previously shown that people do not perfectly optimize their walking speed for energetic cost of transport (Browning and Kram 2005; Seethapathi and Srinivasan 2015). However, these studies also found that the energetic penalty for walking at preferred speed rather than the optimal is normally on the order of 1% of the cost of walking, whereas the net energetic consequences of not adapting to our new cost landscape were several times larger (8% on average). Collectively, these findings suggest that were subjects to initiate optimization, they would have sought to adapt their gait to gain the meaningful savings possible in our new cost landscape.

It is also possible that rapid initiation of optimization requires greater experience than provided here. We attempted to overcome this limitation within our experiment design by matching it to our previous experiment (Selinger et al. 2015). This includes the exoskeleton and its control function, the duration of experience with the new cost landscape, the distance walked during this experience, and the instructions to the subjects. For example, subjects previously initiated optimization in response to 15 min of experience with the new cost landscape, equating to ~1,100 m of walking and 1,600 steps (Selinger et al. 2015). In the current experiment, subjects exceeded this quantity of experience with ~20 min of walking over 2,000 m and ~2,500 steps yet they did not initiate optimization. One possibly important difference between the two studies is that the protocol during the experience phase of the prior experiment encouraged greater variability in step frequency (11 ± 1%) than subjects exhibited naturally here (6 ± 1%). Note that this large value from our prior experiment is the result of low-frequency variability from steady-state holds for several minutes, rather than step-to-step variability, which on a treadmill is relatively small. We suspect, however, that the greater variability of gaits is not the explanation for two reasons. First, the metabolic minimum was still relatively close (<1 SD) to subject's outdoor preferred gait. Second, subsequent treadmill experiments have provided less variable experience and successfully initiated optimization (Selinger JC, Wong JD, Simha SN, Donelan JM, unpublished observations). Importantly, our observations argue against the idea that optimization has initiated but has not had time to complete because we found no consistent shifts in step frequency or speed toward the optimal gait (Fig. 2) suggesting that subjects did not consistently change their behavior and that optimization was thus not consistently initiated. Moreover, there was no overlap of the confidence intervals about final preferred metabolic cost and minimum cost, strongly suggesting that subjects had not begun to minimize energy in our experiment. It is possible that gait optimization had indeed initiated but was below our ability to detect or that only some subjects had begun to optimize.

If not the amount of cost savings, or the amount of experience with the new cost landscape, why did not subjects initiation optimization? We suspect that the answer is that identifying which changes in coordination result in cost savings is a hard problem for the nervous system to rapidly solve in real world walking. A typical walking step deviates from the average preferred gait in many ways. At the level of gait parameters, it may not only have a different step frequency and speed but also a different step width, toe clearance, and maximum knee angle. In addition, at the muscle level, the new step may be accomplished with muscle and motor unit activity patterns that differ in many ways from the average step. Some of these changes to coordination, if performed in isolation, may increase energetic cost, while others may decrease it. Furthermore, whether a particular change in coordination will gain an energetic benefit depends on the walking task: decreasing step frequency, for example, may be beneficial when walking downhill but not when walking on the level. The task to be solved by the nervous system when initiating optimization is to determine which of these many candidate changes to coordination are responsible for sensed reductions in energetic cost and in which contexts. This is often referred to as credit assignment (Minsky 1963; Wolpert et al. 2011). While it is certainly possible to initiate optimization without having determined the coordination dimensions that are responsible for cost savings, this exploration will likely raise cost, rather than lower it, as the majority of coordination changes away from the preferred gait are energetically suboptimal (Kuo and Donelan 2010). Furthermore, even if the nervous system restricts itself to 10 s of high-level gait parameters rather than the activity of 1,000 s of motor units, there remains a large number of dimensions to explore. Evaluating each of these coordination dimensions to determine which result in cost savings requires a large number of walking steps for each new walking context. Rather than purposefully explore, the nervous system may need to rely on behavioral variability to learn the cost-saving coordination dimensions before initiating optimization. However, given the number of candidate dimensions, and the changing walking contexts, this is likely not a rapid process in real world walking. While our previous study's results demonstrated the utility of purposeful exploration to expedite gait optimization, here it appears that step-to-step variability, and the energetic consequences associated with it, may sometimes be disregarded rather than used to initiate and carry out gait optimization. Our results indicate that initiating optimization can take longer than the duration of our experiment, but the observation that people prefer energetically optimal gaits suggests that, if given enough time, the nervous system can optimize in real-world conditions.

Another possibility is that the nervous system's motor objective has many terms, and the primary term for our overground task was not energy minimization. Since subjects in our previous laboratory experiment ultimately preferred to minimize energetic cost, we would also predict energy (and its minimization) to be a major objective for the current study's subjects who walked overground. In addition, in other conditions, other objectives have been proposed. Stability has been proposed to dominate energetic cost under some contexts: when walking downhill, on a treadmill with speed that is controlled to respond to a subject's (noisy) step frequency, or when adapting to a novel exoskeleton (Hunter et al. 2010; Jackson and Collins 2015). In other cases, reduction of ground collision magnitude may be important (Yandell and Zelik 2016; Zelik and Kuo 2012). In reaching tasks, movement accuracy and sensory prediction error may override energetic concerns (Kistemaker et al. 2010, 2014). In this study we have no reason to predict any of these possible objectives to be more important for the overground version of our exoskeleton experiment. Nonetheless, a potential limitation is that outdoor walking may introduce other factors that subjects may wish to minimize or may include periods of walking where energy minimization is weighted less heavily than other concerns (such as stability during decline walking). An added complication with the novel energetic landscape imposed by our exoskeleton control is that the bidirectional torque from the exoskeleton may have made the optimal step frequency vary as a function of incline. Lower step frequencies that were optimal on level ground, because they minimized the negative work done by the exoskeleton, could sometimes have been suboptimal, such as during downhill walking where negative work from the exoskeleton could actually lower metabolic cost. Making the energetic consequences depend on incline, another dimension of variability, may have therefore made learning more difficult. We think that this potential weakness is rather a strength, because the nervous system must regularly weigh the energetic consequences of behavioral policies as it moves the body during ethological movements. The problem of weighing different objectives is the rule, rather than the exception, for the nervous system's optimization of gait.

Finally, our findings may have practical applications to applied motor learning for training and rehabilitation. Our current study demonstrates that that the nervous system cannot always be relied upon to rapidly initiate and perform energy optimization, even when there is meaningful savings to be gained, and even when the range of experience is large. However, our previous study found that the nervous system can reliably and rapidly initiate optimization. We suspect that two differences between the experiments explains this finding. The first is that the context was not continually changing in the prior experiment: the treadmill was level and straight, and the speed was kept constant. This static environment may have allowed the nervous system to understand that all changes to energy costs were due solely to changes in gait and thus determine that cost savings could indeed be gained by changing its control. The second difference is that rather than rely solely on natural variability, like in the current experiments, we instructed subjects in the prior experiment to purposefully explore different step frequencies and enforced them to experience different step frequencies using a metronome. This structured experience and instructions may have helped the nervous system understand the dimensionality of the optimization problem. Both these differences greatly simplify the credit assignment problem for the nervous system. In addition, both these mechanisms, static environment and structured experience, may aid an experimenter, coach, or therapist in speeding the initiation of energy optimization in those learning to use a new device, gain a new skill, or recover after injury or disease.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.D.W., J.C.S., and J.M.D. conceived and designed research; J.D.W. performed experiments; J.D.W. analyzed data; J.D.W., J.C.S., and J.M.D. interpreted results of experiments; J.D.W. prepared figures; J.D.W. drafted manuscript; J.D.W., J.C.S., and J.M.D. edited and revised manuscript; J.D.W., J.C.S., and J.M.D. approved final version of manuscript.

ENDNOTE

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