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RESEARCH ARTICLE

Control of Movement

Increasing the gradient of energetic cost does not initiate adaptation in human walking

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Abstract

When in a new situation, the nervous system may benefit from adapting its control policy. In determining whether or not to initiate this adaptation, the nervous system may rely on some features of the new situation. Here, we tested whether one such feature is salient cost savings. We changed cost saliency by manipulating the gradient of participants' energetic cost landscape during walking. We hypothesized that steeper gradients would cause participants to spontaneously adapt their step frequency to lower costs. To manipulate the gradient, a mechatronic system applied controlled fore-aft forces to the waist of participants as a function of their step frequency as they walked on a treadmill. These forces increased the energetic cost of walking at high step frequencies and reduced it at low step frequencies. We successfully created three cost landscapes of increasing gradients, where the natural variability in participants' step frequency provided cost changes of 3.6% (shallow), 7.2% (intermediate), and 10.2% (steep). Participants did not spontaneously initiate adaptation in response to any of the gradients. Using metronome-guided walking—a previously established protocol for eliciting initiation of adaptation—participants next experienced a step frequency with a lower cost. Participants then adapted by -1.41 ± 0.81 ($P = 0.007$) normalized units away from their originally preferred step frequency obtaining cost savings of $4.80\% \pm 3.12\%$. That participants would adapt under some conditions, but not in response to steeper cost gradients, suggests that the nervous system does not solely rely on the gradient of energetic cost to initiate adaptation in novel situations.

NEW & NOTEWORTHY People can adapt to novel conditions but often require cues to initiate the adaptation. Using a mechatronic system to reshape energetic cost gradients during treadmill walking, we tested whether the nervous system can use information present in the cost gradient to spontaneously initiate adaptation. We found that our participants did not spontaneously initiate adaptation even in the steepest gradient. The nervous system does not rely solely on the cost gradient when initiating adaptation.

energy optimization; explore-exploit; gait; motor learning

INTRODUCTION

We routinely perform movements in a variety of situations. This includes handling of different-sized objects, walking on uneven terrain, or running with fatiguing muscles. Some of these situations are familiar, and for these situations, our nervous system may have already learned an optimal, or near-optimal, control policy (1–3). Here, control policy refers to a mapping between states and actions—the control policy determines what action to take when the system is in any particular state. The optimal control policy is one that minimizes an objective function. In the task of walking on a treadmill, for example, people can rapidly select the step frequency that minimizes energetic cost for each new walking speed (4, 5). In this simple example, energetic cost serves as the objective function, and the optimal

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control policy is the step frequency to be taken at each step to minimize the energetic cost of walking. This rapid selection of step frequency occurs over a few seconds suggesting that the nervous system uses a fast process to choose a control policy that it predicts to be optimal based on prior experience. However, in novel situations, the nervous system has not had the experience to determine whether an existing policy remains optimal, or if a new policy would be better (2, 3). To determine this, the nervous system must adapt the existing policy to a new policy, experience the outcome, and determine whether the new policy results in a lower energetic cost (2, 6). This is a slow process and can take tens to hundreds of seconds. However, if the existing policy remains optimal, then no other policy has a lower cost and any adaptation results in a higher cost. Therefore, even the adaptation to evaluate new control policies is beneficial only when there is a new optimal policy, the presence of which the nervous system does not know in advance. If the old policy remains the optimal policy, then the act of adapting to new policies is itself suboptimal—the nervous system would benefit most by exploiting its existing control policy (7). In this article, we aim to identify a feature of novel situations that cues the human nervous system to initiate adaptation of its control policy.

Our nervous systems do not always initiate adaptation in novel situations. In reaching experiments, people typically initiate adaptation when presented with a force-field that creates a novel relationship between cost and control policy (2, 8). However, when this is followed by another force-field that creates a different novel relationship, the nervous system reverts to erroneously exploiting its original control policy (2, 9). Similar interference to adaptation is also observed in studies that create novel situations using visuomotor rotations or reversals—participants typically can and do adapt to visuomotor rotations and reversals but multiple novel situations can prevent this adaptation (10, 11). In walking tasks, exoskeletons designed to improve walking economy can underperform partly because people are unable to adapt their gait to take full advantage of the benefits that the exoskeleton can offer (12–14). However, participants can and do adapt their gait to obtain larger energetic benefits when they receive experience with different regions of the cost landscape (14, 15). In split-belt walking, although participants typically adapt their step length asymmetry to zero when the two belts move at different speeds, they do not return back to baseline when the speeds of the two belts are changed gradually (16). This suggests that the nervous system relies on particular features of the novel situations to determine if and when to initiate adaptation.
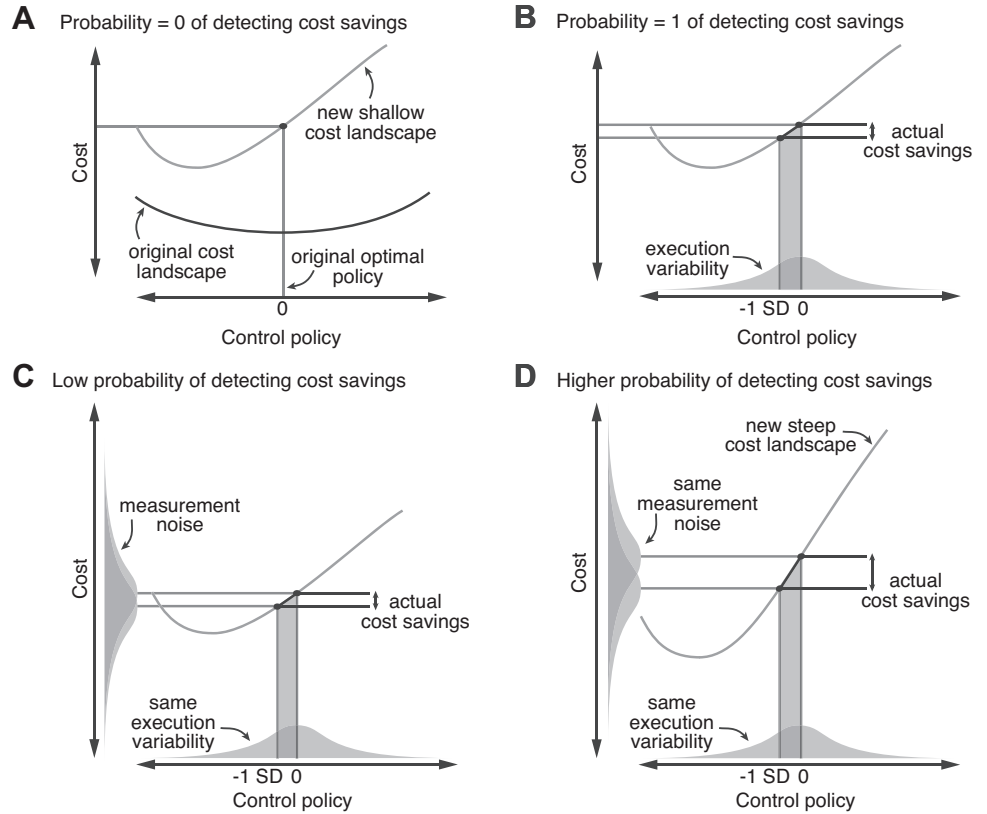
One potential feature used by the nervous system to initiate adaptation is salient cost savings. Here, we use "cost savings" to refer to an improvement in the nervous system's objective function. This may be decreased energetic cost, increased stability, increased accuracy, or some combination of these and other contributors to the objective function. "Saliency" refers to how clear it is to the nervous system that cost savings can be gained, and how it should adapt its control policy to gain the savings. As illustrated in Fig. 1, saliency depends on at least three factors. First, execution variability about the nominal policy—due to either imperfect execution, purposeful exploration, or guidance by an external input—allows the nervous system to experience a greater range of cost savings if they exist (Fig. 1B). Second, measurement noise decreases the ability of the nervous system to discern the presence of cost savings (Fig. 1C). Third, for any given execution variability and measurement noise, an increase in the gradient of the cost landscape increases the ability of the nervous system to discern a cost savings (Fig. 1D). If cost savings are not salient—be it due to any combination of shallow cost gradient, high measurement noise, or low execution variability—the nervous system may choose to exploit its current control policy because whether it should adapt, and if so how it should adapt, is simply not clear.

Recent studies in walking support the premise that the nervous system relies on salient cost savings to initiate adaptation. One of the primary real-time objectives of the nervous system during walking is to minimize energetic cost (15, 17–19). In one of our recent studies, we used robotic exoskeletons to reshape the energetic cost landscape of treadmill walking. Here "cost landscape" refers to the relationship between step frequency and metabolic energetic cost. We reshaped the cost landscape to shift the optimal step frequency to step frequencies lower than normally preferred. Upon their first experience with the new cost landscape, only some participants spontaneously initiated adaptation to the new optimal step frequency. These "spontaneous initiators" had greater step frequency variability than the "nonspontaneous initiators" who persisted walking at the previous optimal step frequency. This suggests that the naturally higher variability increased the saliency of the cost savings to the nervous system which led to the initiation of adaptation. We were also able to prompt the nonspontaneous initiators to initiate adaptation by providing them with experience with step frequencies that resulted in a lower energetic cost. One interpretation of this result is that the experience increased the saliency of the energetic cost savings for the nervous system causing it to initiate further exploration. Counter to these findings, we did not find that increased gait variability was sufficient to initiate adaptation in a subsequent study on over ground walking (13). When compared with our treadmill studies, changes in cost in this over ground study were due not only to changes in step frequency, but also speed and terrain. We suspect that the nervous system did not initiate adaptation within the duration of this over ground experiment because the added dimensionality increased the complexity of the credit assignment problem making it difficult for the nervous system to determine which energetic changes could be attributed to its control and which were due to the differences in terrain.

In the present study, we aimed to test whether the saliency of energetic cost savings is a feature that the nervous system uses to initiate adaptation in human walking. To accomplish this, rather than manipulate measurement noise or movement variability, we changed saliency by manipulating the gradient of the energetic cost landscape. We manipulated the gradient using a mechatronic system that applied controlled fore-aft forces to the waist of participants as they walked on a treadmill. These applied forces were a function of participants' step frequency and acted to increase energetic cost at high step frequencies and reduce it at low step frequencies. By making the forces a function of only step

Figure 1. Conceptual representation of how the nervous system might detect cost savings from a cost landscape. *A*: the nervous system is introduced to a novel situation where the relationship between the control policy and cost has changed (black to gray curve) such that the original optimal policy is no longer optimal. With exact execution and measurement, the nervous system cannot detect any cost savings in the new landscape. *B*: execution variability—illustrated by the horizontally aligned Gaussian distribution—allows the nervous system to exactly experience the lower costs relative to the original policy, making the energetic cost savings salient. *C*: the presence of measurement noise—illustrated by the two vertically-aligned Gaussian distributions centered on the means of the two cost measurements—can reduce saliency by reducing the probability that the nervous system can detect a cost savings. In this example, the cost measurement means are close, and the cost measurement noise distributions are wide resulting in a low probability that the nervous system will detect a cost savings for the given execution variability. *D*: an increased gradient can increase the probability of detecting cost savings and thus increase the saliency of a cost landscape for the same execution variability and measurement noise.

frequency and keeping the walking speed constant, we aimed to only affect the gradient of the step frequency cost landscape, indirectly signaling to the nervous system how it should adapt its control policy to obtain cost savings. We increased the gradient of the cost landscape about participants' originally preferred step frequency by increasing the magnitude of force change that the system provided for a given change in step frequency. We hypothesized that increasing the gradient of the cost landscape will cause participants to spontaneously initiate adaptation of their step frequency.

METHODS

Experimental Design

We manipulated cost landscapes using our recently developed mechatronic system (Fig. 2A). We describe this system in detail in our earlier paper (19). Briefly, it
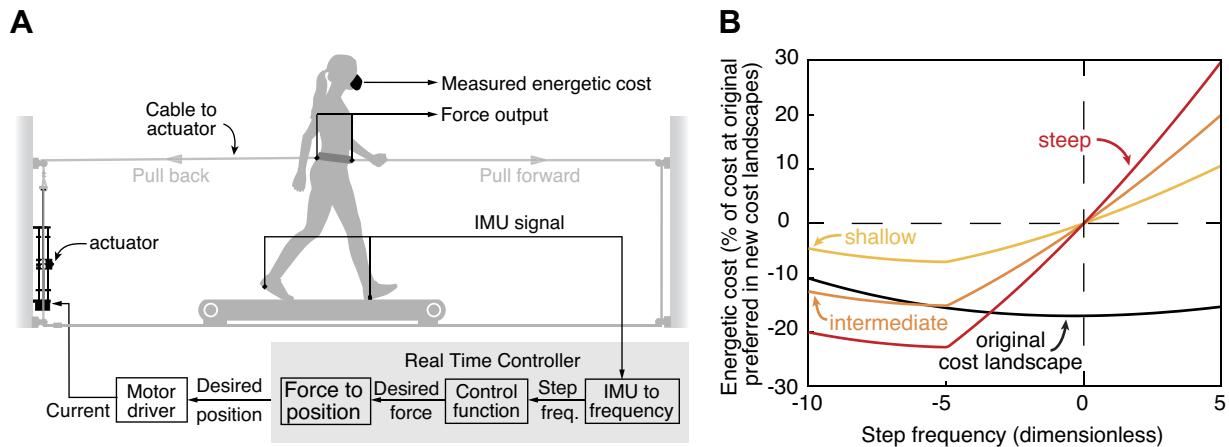

Figure 2. *A*: participants walked in a mechatronic system that applied controlled fore-aft forces as a function of their walking step frequency. Backward forces provided an energetic penalty, raising the cost of walking relative to normal. Moderate forward forces provided an energetic reward, lowering energetic cost. Reused with permission from Simha et al. (19). *B*: using simulations, we predicted that participants would experience cost landscapes with gradients of 1.4 (shallow), 2.8 (intermediate), and 4.2 (steep) percentage change in cost per unit change in step frequency, about their originally preferred step frequency (0).

manipulates a participant's original cost landscape by applying fore-aft forces to their waist while they walk on a treadmill. The controller specifies the forces as a function of the participant's step frequency. Backward forces increase the energetic cost associated with the executed step frequency, relative to normal, while moderate forward forces decrease the energetic cost (20). The system uses inertial measurement units (IMU) placed on participants' feet to detect ground contact events, and this signal is processed by a real-time controller to determine the participants' executed "step frequency," defined as the inverse of the time elapsed between left and right foot ground contact events. We provide the controller with a "control function" that defines the relationship it has to maintain between the measured step frequency and the applied force. Based on this control function and the measured step frequency, the controller commands the required force for each new step to an actuator via a motor driver. The force applied by the actuator is transmitted to the participants through long tensioned cables that are attached to a hip belt, and we monitor that force using force transducers in-line with the front and back cables.

We tested participants' behavior in cost landscapes of three different gradients. Using data from literature, we can predict for an average participant the energetic cost associated with each step frequency when walking without any external force (21) and the energetic cost of walking when a range of fore-aft forces are applied but at a fixed step frequency (20). We combined these relationships to predict the cost landscapes created by a control function (19). Using these simulations, we designed three control functions—"shallow," "intermediate," and "steep"—that created cost landscapes of three different gradients (Fig. 2B).

$$F_{shallow} = \begin{cases} -0.07 \cdot sf - 1.36, & sf \leq -5 \\ -0.19 \cdot sf - 1.98, & sf > -5 \end{cases} \quad (1)$$

$$F_{intermediate} = \begin{cases} -0.07 \cdot sf - 0.40, & sf \leq -5 \\ -0.39 \cdot sf - 1.98, & sf > -5 \end{cases} \quad (2)$$

$$F_{steep} = \begin{cases} -0.07 \cdot sf + 0.56, & sf \leq -5 \\ -0.58 \cdot sf - 1.98, & sf > -5 \end{cases} \quad (3)$$

Here, sf is a normalized step frequency and is dimensionless. To perform this normalization, we first measured the average step frequency originally preferred by each participant during a baseline trial (cf., *Experimental Protocol*), as well as the standard deviation in step frequency about this average preferred step frequency. We then calculated the normalized step frequency for each step in the subsequent trials by subtracting the average originally preferred step frequency from each step's measured step frequency and then dividing by the standard deviation about the originally preferred step frequency. This normalization controls for the differences between participants in their step frequency variability, which is normally one of the contributors to the saliency of cost savings. It also forces measured step frequencies

that are equal to the originally preferred step frequency to evaluate to 0. Designing cost landscapes using this normalization is independent of how the nervous system senses cost savings because even if the nervous system senses absolute cost savings, it will sense increasingly larger cost savings going from the shallow to steep cost gradient. We normalized the forces applied to a participant by their body weight. In *Eqs. 1–3*, the intercepts, slopes, and the forces all have units of percent body weight (sf is dimensionless). We designed the control function for the shallow cost landscape to match that used in Simha et al. (19) with a cost gradient of 1.4 about the originally preferred step frequency. We chose this for the shallow cost landscape because participants did not spontaneously initiate adaptation in Simha et al. but did so after experiencing cost savings—making it the ideal cost landscape to steepen to test our hypothesis here. We designed the other control functions to generate steeper cost landscapes, with cost gradients of 2.8, and 4.2 about the originally preferred step frequency, while otherwise matching the shallow cost landscape. These gradients have units of percent change in energetic cost for a unit change in normalized step frequency. For example, were a participant walking in the intermediate gradient condition to choose a step frequency 1 normalized unit lower than their originally preferred step frequency, the participant will experience a 2.8% reduction in energetic cost relative to what they experienced at the originally preferred step frequency. For comparison, the cost landscape used in Selinger's study roughly corresponds to the shallowest gradient we use here (15, 18). To experience a cost gradient as steep as our steepest, one would have to walk at a step frequency roughly 7.5% higher than their preferred step frequency in their original cost landscape (21). We designed all the new cost landscapes to have the same cost at the originally preferred step frequency. This helped ensure that when we changed the cost landscape, participants only experienced the gradient change, without experiencing any change in the average steady-state cost. As different nervous systems can respond differently to our control functions, each participant may not experience exactly the cost landscape that we aimed to create. However, our prior results show that, on average, we are able to accurately create our designed cost landscapes (19).

Before conducting the experiment, we wanted our experimental design to meet three criteria. First, we tested whether any adaptation we observe could be a consequence of walking with a backward force. Contradictory to this hypothesis, we examined data from pilot studies and found no relationship between walking step frequency and backward forces at the hip ($n = 20$). Recent results from a different research group support this finding (22). Second, we determined that execution variability is not systematically impacted by the different cost gradient conditions. On average, the step-to-step variability in self-selected step frequency was not different between walking in two different cost gradients ($n = 9, 8$; unpaired t test; $P = 0.69$) nor was the slope of the line relating the step-to-step variability in step frequency with a range of commanded forces significantly different from zero ($n = 11$; linear mixed effects model: avg slope $= -0.02$, $P =$

0.08). Finally, we determined that the forces applied by the mechatronic system do not contribute to a change in measurement noise across the gradient conditions based on the following metrics: the mechatronic system commands forces with an average rise time of 85 ms which is less than 25% of a typical walking step frequency of 125 steps/min, the RMSE of force is 0.59% body weight (19), and the slope of the line relating this variability to the magnitude of the applied force was not significantly different from zero ($n = 11$; linear mixed effects model: avg slope = -0.002, $P = 0.83$).

Experimental Protocol

We collected data from 11 naïve participants (means ± SD; age: 24 ± 3 yr; height: 167 ± 11 cm; mass: 68 ± 11 kg; sex: 5 females, 6 males). All participants were healthy and had no known history of cardiopulmonary or gait impairments. The study protocol was approved by the Simon Fraser University Research Ethics Board and all participants gave written informed consent before participation. To a priori determine the sample size necessary to evaluate our hypothesis, we first performed a pilot experiment where we measured a group of 8 participants' preferred step frequency in a new cost landscape. We observed a group standard deviation of 1.01 steps/min. Using MATLAB's sampsizepwr function, we then estimated that 11 participants will allow a one-tailed Student's t test ($\alpha = 0.05$, $1 - \beta = 0.90$) to detect an average change of 1 normalized unit in step frequency.

Each participant completed four periods of walking on the same day (Fig. 3). Before the beginning of these four experimental periods, all participants spent ~10 min habituating to walking on our treadmill at a speed of 1.25 m·s^{-1}. During this habituation, we instructed them to walk with both short and long steps. They were not attached to the mechatronic system. This was followed by the first period of the experiment where participants walked for 9 min while attached to the mechatronic system. We used data from this period to quantify the characteristics of their baseline walking step frequency. During this time, the system controlled for a target applied force of 0 N (Fig. 3A). We calculated the average and standard deviation of their step frequency from the 6th to 9th min to parameterize the step frequency in future trials. We refer to this average as the "originally preferred step frequency" and the standard deviation as "original step frequency variability."

In the second period, we tested whether participants would spontaneously initiate adaptation in the shallow and steep gradients (Fig. 3B). They experienced 0 N for the first 30 s to allow them to reach a steady-state step frequency (4). We programmed the system to ramp up the force over the next minute (*min 0.5–1.5*) to the force that would be applied at the participants' originally preferred step frequency in the new cost landscapes. This ensured that participants were not perturbed by a sudden change in force when the cost landscape changed. This force was held constant for 30 s (*min 1.5–2*; "shallow prespontaneous"). The controller then engaged the control function for the shallow gradient, and participants walked at a self-selected step frequency for 5 min (*min 2–7*; "shallow spontaneous"). Then the controller switched to the steep gradient. Once again, we ensured that participants were not perturbed during the cost landscape transition by constraining the rate at which the force could change for 30 s (*min 7–7.5*). Participants then self-selected their step frequency for 5 min (*min 7.5–12.5*; "steep spontaneous"). To avoid fatigue, we then provided a break of 5–10 min before beginning the third period. For each participant, we averaged their self-selected step frequency over the last 30 s of walking in each gradient to determine their "spontaneous adaptation" in that gradient ("shallow spontaneous": *min 6.5–7*; "steep spontaneous": *min 12–12.5*).
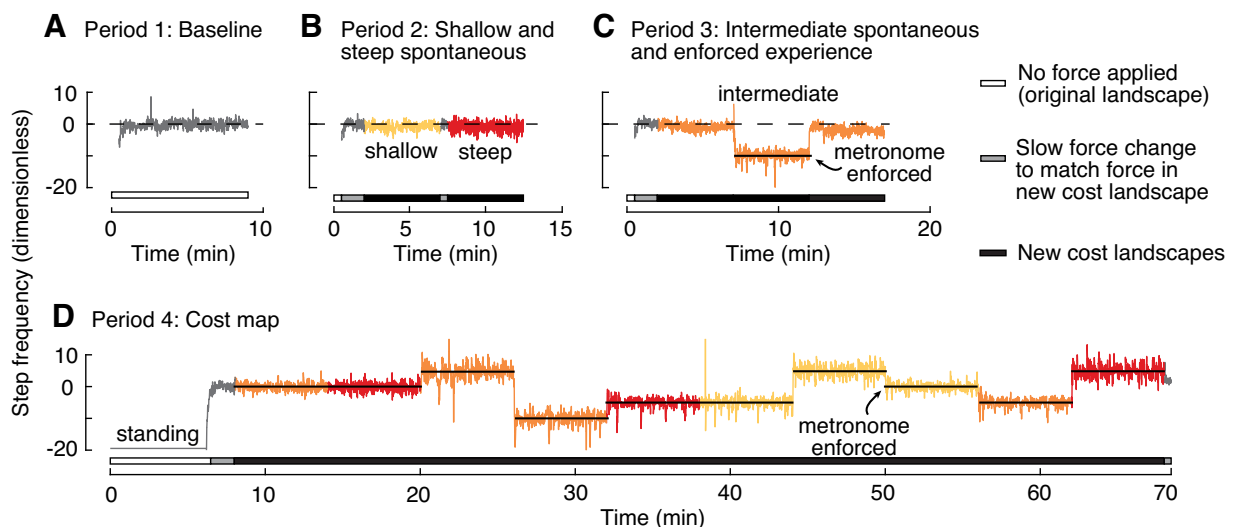

Figure 3. Step frequency measured from a representative participant during the different walking periods. Each participant completed four periods of walking in a single day ($n = 11$, 5 females, 6 males). A: first, they walked for 9 min as the system controlled for a force of 0 N to be applied to their waist. We used this baseline period to estimate their average original preferred step frequency and original step frequency variability. B: then participants walked for 5 min each in the shallow and steep gradients to test for spontaneous adaptation. C: in the third period, participants walked in an intermediate gradient. We used this condition to test for both spontaneous adaptation to an intermediate gradient and adaptation after enforced experience with a low cost. D: finally, we measured the actual gradients experienced by participants in each the cost landscapes.

We used the third period to test for adaptation in an intermediate gradient (Fig. 3C). The first part of this period served as a sort of Goldilocks test in the event that the shallow and steep gradients were both perceived as extreme by the nervous system (23)—too shallow a gradient may not provide salient cost savings whereas too steep a gradient might be interpreted as noise or challenge to stability despite providing salient cost savings. Similar to the second period, the force was ramped up in the first 2 min to prevent perturbing forces. The controller then engaged the control function for the intermediate gradient, and participants self-selected their step frequency for 5 min (*min 2–7*; "intermediate spontaneous"). One possible outcome of our experiment was that participants would not spontaneously adapt in any of the gradients. With this outcome, we would not be able to distinguish between the possibility that participants will adapt but not spontaneously, and the possibility that participants would not adapt at all in our system with our experimental paradigm. Therefore, the next part of this experimental period was to verify whether adaptation was possible at all. Prior work has shown that experiencing a lower cost in a new cost landscape is sufficient to cause the nervous system to initiate adaptation (18). Using this principle, we next required participants to match their step frequency to an audio metronome that played a frequency −10 normalized units away from their originally preferred step frequency. According to our designed cost landscape, we expected this step frequency to provide a cost savings of 12.5% relative to the cost at 0. After 5 min of matching the metronome (*min 7–12*; "intermediate metronome guided"), the metronome was turned off and participants self-selected their step frequency for another 5 min (*min 12–17*; "intermediate postexperience"). Once again, we averaged each participant's step frequency during the last 30 s of each condition to determine their preferred step frequency in that condition ("intermediate spontaneous": *min 6.5–7*; "intermediate postexperience": *min 16.5–17*). Note that spontaneous initiation of adaptation is tested only during the second and third walking periods which last 12.5 min and 17 min, respectively, with a 5–10 min break in between, to ensure that fatigue does not affect execution variability, measurement noise or the adaptation process.

The purpose of the fourth period was to measure the actual energetic cost experienced by the participants in each of the new cost landscapes ("cost mapping"; Fig. 3D). Importantly, this always occurred after the adaptation period to ensure that participants were naïve to the cost landscapes when we tested for adaptation. During this period, participants were also instrumented with a respiratory gas analysis system (Vmax Encore Metabolic Cart, Viasys, PA). They spent the first 6 min standing still while we measured their resting metabolic rate (*min 0–6*). They then started walking while the mechatronic system maintained a force of 0 N to allow them to reach a steady-state gait (*min 6–7*). Following this, participants walked at specific walking conditions chosen to allow us to estimate the gradient about the originally preferred step frequency in each of the cost landscapes, and also to estimate if the "experience low" period indeed allowed participants to experience a lower cost. Participants walked in 10 conditions total: step frequencies of 0, −5, and +5 in shallow, intermediate, and steep

gradients, and −10 in only the intermediate gradient. We enforced this by instructing participants to match an audio metronome that played these frequencies. We programmed the controller to present these conditions in a random order to each participant, to prevent any order effects on these metabolic energy measures. To determine energetic cost, we measured the total volume of oxygen consumed and volume of carbon dioxide produced in the last 3 min of each condition, and divided them by the duration over which they were measured, to obtain the steady state average rates of oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$). We then estimated the metabolic rate using the following equation (24–26):

$$P_{met,gross} = \left(16.48 \frac{W\,s}{ml\,O_2} \dot{V}_{O_2}\right) + \left(4.48 \frac{W\,s}{ml\,CO_2} \dot{V}_{CO_2}\right). \quad (4)$$

We subtracted resting metabolic power for each participant and present net energetic cost as the energy used per unit time normalized for the person's body mass. It has the units $W{\cdot}kg^{-1}$.

Data Analysis

We first determined the average gradients and metronome-guided cost that participants experienced in each cost landscape. We used MATLAB's fitlm command to find the best linear fit through the energetic costs at −5, 0, +5 normalized step frequencies for each participant, in each cost landscape. We define the cost landscape gradient for each participant as the slope of this fit. We also used a one-tailed paired Student's t test to determine whether the cost at a step frequency of −10, where we held participants during the "intermediate metronome-guided" condition, is lower than the cost at a step frequency of 0 in the intermediate gradient. To determine the location of the cost minimum and the magnitude of cost savings obtainable at the minimum, we also fit a quadratic relationship to the costs measured in the intermediate gradient condition for each participant.

We evaluated whether participants spontaneously initiated adaptation in response to steeper gradients. We first compared the preferred step frequency in the shallow gradient with the originally preferred step frequency using a one-tailed Student's t test. We found that these values were indeed different, but we did not attribute this shift in preferred step frequency to an adaptation in response to a new cost gradient (cf., RESULTS). To determine if there was any additional changes in preferred step frequency in the steeper gradients, we then compared the average step frequencies during the spontaneous adaptation periods in the intermediate and steep gradient to the same period in the shallow gradient.

We also determined whether participants initiated adaptation after enforced experience with a low cost. We used a one-tailed paired Student's t test to determine whether participants' preferred step frequency after the "intermediate metronome-guided" condition was significantly lower than the average step frequency 30 s before the experience with low cost. The step frequency in this 30 s before the experience corresponds to the spontaneous adaptation in the intermediate gradient, allowing us to determine whether the metronome-guided experience generated adaptation that did not occur spontaneously.

In the conditions where we observed adaptation, we characterized the rate of adaptation. We did so because a preferred step frequency can arise from fast predictive processes that can occur over a few seconds or optimization processes that can occur over tens or hundreds of seconds (4). As described in the INTRODUCTION, we are interested in the slow process since it is indicative of the nervous system learning to adapt its policy to a novel situation. We modeled each participant's adaptation of step frequency over time as a two-process exponential. We first averaged the step frequency during the last 30 s before the beginning of the condition of interest, and the step frequency during the last 30 s of the condition. If these two averages were different, we normalized the step frequency data during that condition such that the average step frequency of the 30 s before the condition evaluated to 0, and the average of the last 30 s evaluated to 1. We then used least squares regression implemented through MATLAB's fitnlm function to model these data as the sum of two exponentials (4). We used the time constants from this model to estimate the duration of the optimization process.
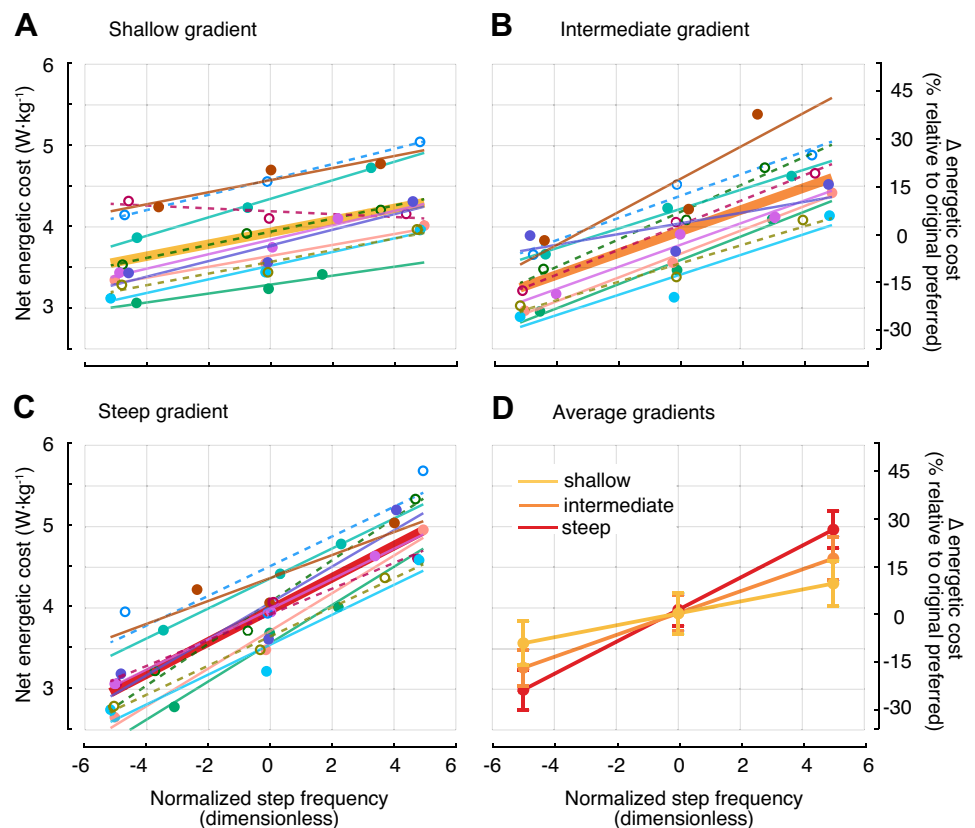
RESULTS

We were successful in creating cost landscapes of different gradients. We found that participants on average experienced a shallow gradient of 0.07 ± 0.03 W·kg^{-1} (means ± SD), an intermediate gradient of 0.14 ± 0.03 W·kg^{-1} and a steep gradient of 0.20 ± 0.04 W·kg^{-1} (Fig. 4). This is calculated as the change in energetic cost per normalized unit of step frequency. We use 1 standard deviation of participants' preferred step frequency in their original cost landscape, to normalize the measured step frequency. This means that participants experience the reported gradient through a variability of 0.5 standard deviations higher and lower than their originally preferred step frequency. Thus, 1 standard deviation higher and lower than their originally preferred step frequency, which accounts for 68% of their steps, would have allowed participants to experience a change in energetic cost of 3.6%, 7.2%, and 10.2% in the shallow, intermediate, and steep gradients, respectively. We also found that when participants in the intermediate gradient were held −10 normalized step frequencies lower than their originally preferred step frequency, they experienced an average cost savings of 8.1%±9.1% relative to the cost at the originally preferred step frequency ($P = 0.006$). From the quadratic relationship we fit to the same cost landscape, we estimate that, on average, the cost minimum occurred −6.1 normalized units away from participants' originally preferred step frequency, providing a cost savings of 10.8%.

Participants did not spontaneously initiate adaptation in response to steeper cost gradients. In the second period, participants first experienced the shallow cost landscape, and then the steep cost landscape. They walked freely at their self-selected step frequency for 5 min in both cost landscapes. The average step frequency from the last 30 s of the shallow period was lower than the original preferred step frequency (−0.69 ± 0.82 vs. 0; $P = 0.01$). However, this step frequency was indistinguishable from the average step

Figure 4. Shallow (*A*) intermediate (*B*), and steep gradients (*C*). Each filled/open circle represents one measurement from one participant. Thin solid/dashed lines are linear fits to each participant's cost measurements (*n* = 11, 5 females, 6 males). Data points and best-fit lines from a given participant are presented in a single color. Some colors are presented using the combination of dashed line-open circles to distinguish them from similar colored solid line-filled circles. Thick lines are the average of the individual linear fits. *D*: on average the gradients are increasing from shallow to steep. The filled circles represent the average cost measures at the commanded step frequencies, and the error bars represent the 95% confidence interval of the same.

frequency preferred by participants during the 30 s before the beginning of the shallow gradient (Fig. 5; shallow prespontaneous vs. shallow spontaneous; -1.02 ± 0.64 vs. -0.69 ± 0.82, respectively; $P = 0.33$). Therefore, we do not interpret this to be an initiation of adaptation toward the optimal policy. When the system switched from the shallow landscape to the steep landscape, participants still did not initiate adaptation, and preferred a step frequency (Fig. 5; steep spontaneous; -0.76 ± 0.99) that was indistinguishable from that preferred in the shallow cost landscape (Fig. 5; shallow spontaneous; -0.69 ± 0.82; $P = 0.40$). Our goldilocks test with the intermediate gradient also resulted in preferred step frequencies that were indistinguishable from that preferred in the shallow landscape (Fig. 5; shallow spontaneous vs. intermediate spontaneous; -0.69 ± 0.82 vs. -0.74 ± 0.82; $P = 0.43$).

Participants did, however, initiate adaptation after enforced experience with a lower cost. We allowed participants to self-select their step frequency after matching a metronome that held them at a step frequency that had a cost lower than the cost at 0 in the intermediate cost landscape. On average, participants adapted by -1.41 ± 0.81 toward the new cost minimum (Fig. 5; intermediate postexperience). This adaptation was to step frequencies significantly lower than that spontaneously preferred in the intermediate gradient ($P = 0.007$). It led to average cost savings of $4.80\% \pm 3.12\%$ relative to the cost at 0. This was an average cost savings of $2.46\% \pm 2.92\%$ relative to the cost experienced at the end of the intermediate

spontaneous period. We found that the time course of the change in step frequency of most participants was captured well with a two-process exponential model (RMSE $= 0.16 \pm 0.08$; $R^2 = 0.36 \pm 0.21$). The time constant of the fast process was 4.4 ± 2.5 s whereas that of the slow process was 190.2 ± 209 s. We interpret the presence of this slow process as evidence that the nervous system indeed initiated adaptation in response to the enforced experience with a lower cost gait.

DISCUSSION

Contrary to our hypothesis, steeper gradients did not lead to spontaneous initiation of adaptation. This null finding is not because our methods were unsuccessful in creating gradients of increasing steepness. We used our cost mapping trials to verify that the participants did indeed experience three different gradients—the intermediate and steep gradients were ~twofold and threefold the shallow gradient, respectively. The lack of initiation also does not appear to be a consequence of the rapid exposure to multiple gradient conditions preventing the nervous system from attempting any adaptation. We verified this by leveraging results from previous studies that found that adaptation can be initiated by guiding the nervous system to experience a cost lower than the cost at the originally preferred step frequency (18). We did the same here and found that participants could indeed initiate adaptation in the intermediate landscape after such experience, despite the intermediate landscape being the third landscape experienced by participants. When considered together, these results suggest that either the nervous system does not use salient cost savings to initiate adaptation, or that the cost savings were not salient to the nervous system in our experiment.

For savings to be salient, the nervous system needs to both detect that cost savings can be gained and determine how it should adapt its control policy to gain the savings. In our experiment, energetic cost per unit time is equivalent to energetic cost per unit distance as the walking speed is constant throughout the experiment. Therefore, participants did experience the increasing cost gradients irrespective of how energetic cost is represented in the nervous system's objective function. However, depending upon how the nervous system senses energetic cost, it may be challenging for the nervous system to detect cost savings from the cost landscape gradient. For example, one possible sensory system for estimating energetic cost involves the ergoreceptors that are sensitive to the slow build-up, or slow reduction, of muscle metabolic byproducts (27–29). This build-up creates a sensory response that is an integration of the effect of many steps, rather than one that closely follows the step-to-step changes in energetic cost. It will be more difficult for the nervous system to detect a gradient in cost landscape from the step-to-step variability in energetic cost when using this mechanism because integration has the effect of decreasing the sensed gradient, perhaps even to zero if the build-up is particularly slow. This, or a similar integrative sensing mechanism, may be why metronome-guided experience is effective at initiating adaptation—the metronome holds participants at a lower cost for many steps allowing time for integration. However, some participants in some conditions are able to use the step-to-step variability in energetic cost to
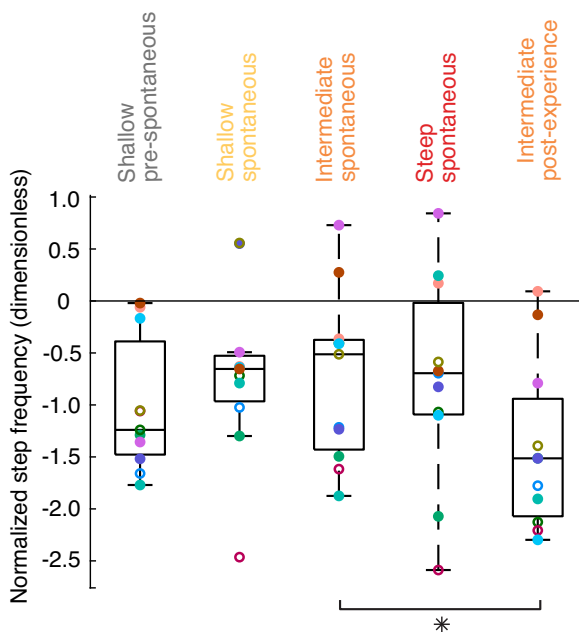

Figure 5. Average spontaneous adaptation in the shallow gradient was indistinguishable from participants' preferred step frequency just prior to the beginning of the shallow cost landscape ($n = 11$, 5 females, 6 males; means $\pm$ SD; shallow prespontaneous vs. shallow spontaneous: paired t test, $P = 0.33$). The spontaneous adaptation in all gradients were also indistinguishable from each other after 5 min of walking (shallow spontaneous vs. intermediate spontaneous: paired t test, $P = 0.43$; shallow spontaneous vs. steep spontaneous: paired t test, $P = 0.40$). However, after experience with a lower cost in the intermediate gradient, participants preferred to walk at a significantly lower step frequency (intermediate spontaneous vs. intermediate post-experience: paired t test, $P = 0.007$).

spontaneously initiate adaptation (18). This suggests that if a slow sensing system does indeed play a role in estimating energetic cost, it is not the only contributing system. It may also be that the nervous system uses proxies, such as muscle activation, to estimate energetic cost and these estimates may not accurately capture the global energetic cost changes observed in this experiment.

Another possibility for the lack of initiation of adaptation is that the gradients allowed participants' nervous systems to sense the presence of cost savings but not how to adapt their control policy to obtain those savings. That is, the nervous system has difficulty with credit assignment in our experiment (30). We manipulated the cost gradient associated with only one gait parameter—step frequency—to allow the nervous system to detect an increase in cost savings and detect the gait parameter to adapt to obtain those savings. However, when walking in our system, we suspect that it is not clear to most participants that the backward force depends on any aspect of their gait, including their step frequency. It appears to be challenging for the nervous system to identify salient cost savings using the structure of natural variability in gait to determine the gradient of a cost landscape—a finding consistent with our earlier experiment studying adaptation in over ground walking (13). Although we do not suspect that the adaptation in this experiment is an explicit strategy, perhaps explicit cues may aid in the initiation of adaptation. Metronome-guided experience of step frequencies with lower cost may provide the nervous system with such an explicit association between the cost savings and the changes to control policy that provide those cost savings. Similarly, reaching experiments have found that presenting participants with multiple different force-fields interferes with learning, but that such interference can be overcome with certain contextual cues such as follow through movements or cues that associate a change in the optimal control policy with another change such as spatial location of movement (31, 32). Differences in contextual cues might explain why it was easier for the nervous system to identify that there was a relationship between step frequency and the changes to knee torque for some participants in our previous experiment than with step frequency and torso forces in the present experiment (18). This interpretation is consistent with recent study in visuomotor adaptation that found that implicit and explicit learning work together to improve adaptation (33).

Although we designed our custom-built equipment and our protocol to meet the requirement for energetic cost saliency, our experiment nevertheless had limitations. Toward this requirement, the maximum cost savings that participants experienced from their variability in step frequency, relative to the cost at their originally preferred step frequency, was 5.1% in the steep gradient. In contrast, participants experienced cost savings of 8.2% during their metronome-guided lower cost experience in the intermediate gradient. This suggests that even the steep gradient may not have allowed participants to experience a large enough cost savings. However, we suspect this is not the case because in our previous study with the shallow gradient, participants initiated adaptation after experiencing cost savings of only 3.5% through similar metronome-guided walking (19). This earlier cost savings was smaller than that

experienced by our current participants in the steep gradient condition suggesting that the currently experienced cost savings, at least in the steep gradient condition, were sufficiently large for the nervous system to detect.

A second limitation is that our experimental design resulted in participants preferring step frequencies slightly lower than the original preferred step frequencies in all gradient conditions (Fig. 5). We do not interpret these shifts as evidence of the initiation of energetic cost optimization in response to new cost landscapes. Our rationale is that participants were already walking at shifted step frequency during the 30 s before the beginning of each new cost landscape (shallow: -1.02 ± 0.64, intermediate: -0.25 ± 0.63, steep: -0.62 ± 0.54). Why is step frequency shifted lower than the baseline measures both before and during the experience with the new cost landscapes? One possible explanation is that we may not have provided a long enough baseline period for participants to settle into their preferred step frequency. However, others have found that 2 min of walking is sufficient for stride frequency to reach steady state—we provided 9 min (34, 35). A second possible explanation for the presence of these shifts may be the net backward force that participants experienced both immediately before and during the cost landscape, but not during the baseline phase when the net force was zero. Our system slowly ramped up the backward force to those which participants would experience in the new cost landscapes at their originally preferred step frequency. The force was then held constant for 30 s before the controller switched to the new cost landscapes and our step frequency estimate before the beginning of the new cost landscape is from this constant-force period. However, concerned about the possible role of net backward force on step frequency, we performed pilot experiments before our reported experiments and found no relationship. In support of our pilot results, a recent study also found that backward forces do not have an effect on stride period (22). Furthermore, walking uphill, which is biomechanically similar to experiencing a net backward force, also results in step frequencies that are not significantly different from walking on level (36). Further research will be required to understand why we observed this consistent shift in step frequency.

After metronome-guided experience, our participants did not converge on the energy minimal step frequency. Participants adapted toward the energy minimum, that was also toward the step frequency that they walked at during the metronome-guided experience. One interpretation of this could be that the adapted step frequency was an after-effect of the metronome-guided experience. Contrary to this, previous studies, including a study with the same mechatronic system and shallow cost landscape used in this study, found that participants rapidly return to their originally preferred step frequency without after-effects when released from higher step frequencies when they correspond to a higher cost (15, 17–19). Another interpretation may be that forces to the hip cause the nervous system to prioritize stability. However, Joshi and Srinivasan (37) found that when walking is perturbed in the fore-aft direction using backward forces to the hip, participants prefer to walk with a higher step frequency, contrary to what we observe here. We estimate that in our present study, on average, participants could have obtained a cost savings of 10.8% if they had

shifted their step frequency −6.1 normalized units away from their originally preferred step frequency. Yet we found that participants only adapted their step frequency by −1.4 ± 0.8 to obtain a cost savings of 4.83% ± 3.61%. This was only 2.46% ± 2.92% additional savings relative to the cost experienced at the end of the intermediate spontaneous period. This might suggest to some that energetic cost savings do not play a role in the adaptation of step frequency in the cost landscapes we used. We suspect that this is not the case since participants did adapt after experience with a lower energetic cost. This cost savings obtained from the adaptation, while small and variable between participants, was still consistent among participants, and the magnitude of savings comparable to previous studies (15, 19). One candidate explanation is that the nervous system seeks to minimize an objective function that is a combination of energetic cost, stability, accuracy, and other contributors (17). The minimum of this combined cost function may coincide with the final preferred step frequency and not with the energetic cost minimum. Alternatively, as mentioned earlier, it is possible that the nervous system uses proxies to estimate global energetic cost whose minima do not coincide with the global energetic minimum in this experiment.

In conclusion, the nervous system does not solely rely on the gradient of energetic cost to initiate adaptation in novel situations. As we and others have previously found, explicit experience with more optimal movements can assist with the initiation of adaptation. A better understanding of the interplay between implicit and explicit experience for the nervous system to initiate adaptation when the saliency of cost savings is not apparent may help improve rehabilitation for those recovering from injuries, help coaches speed up training with new techniques, or aid scientists looking to study adaptation in complex novel environments.

GRANTS

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

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