



## 36 **Introduction**

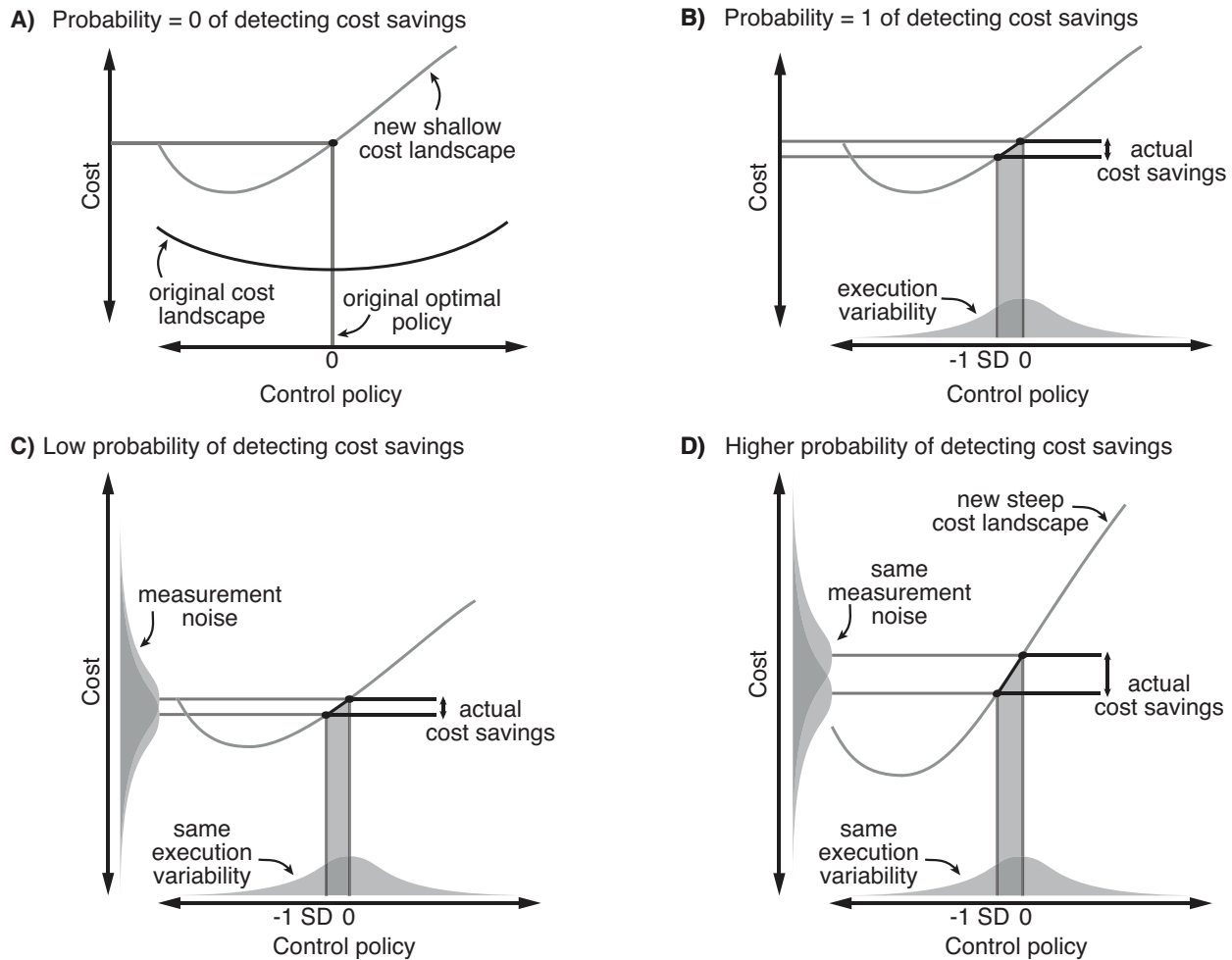
37 We routinely perform movements in a variety of situations. This includes handling of  
38 different-sized objects, walking on uneven terrain, or running with fatiguing muscles. Some  
39 of these situations are familiar, and for these situations, our nervous system may have  
40 already learned an optimal, or near-optimal, control policy (Izawa et al., 2008; Wolpert et  
41 al., 2011; Wolpert and Flanagan, 2016). In the task of walking on a treadmill, for example,  
42 people can rapidly select the step frequency that minimizes energetic cost for each new  
43 walking speed (Pagliara et al., 2014; Snaterse et al., 2011). But in novel situations, the  
44 nervous system hasn't had the experience to determine whether an existing policy remains  
45 optimal, or if a new policy would be better (Wolpert et al., 2011; Wolpert and Flanagan,  
46 2016). To determine this, the nervous system must adapt the existing policy and  
47 experience the outcome (Sutton et al., 1992; Wolpert et al., 2011). This adaptation is  
48 beneficial only when there is a new optimal solution, the presence of which the nervous  
49 system does not know in advance. If the old policy remains the optimal policy, then the act  
50 of adapting to new policies is itself sub-optimal—the nervous system would benefit most  
51 by exploiting its existing control policy (Sutton et al., 2017). In this paper, we aim to  
52 identify a feature of novel situations that cues the human nervous system to initiate  
53 adaptation of its control policy.

54  
55 Our nervous systems do not always initiate adaptation in novel situations. In reaching  
56 experiments, people typically initiate adaptation when presented with a force-field that  
57 creates a novel relationship between cost and control policy (Shadmehr and Mussa-Ivaldi,  
58 1994; Wolpert et al., 2011). However, when this is followed by another force-field that  
59 creates a different novel relationship, the nervous system reverts to erroneously exploiting  
60 its original control policy (Gupta and Ashe, 2007; Wolpert et al., 2011). Similar interference  
61 to adaptation is also observed in studies that create novel situations using visuomotor  
62 rotations or reversals (Krakauer et al., 2019). In walking tasks, exoskeletons designed to  
63 improve walking economy can underperform partly because people are unable to adapt  
64 their gait to take full advantage of the benefits that the exoskeleton can offer (Jackson and  
65 Collins, 2015; Wong et al., 2019; Zhang et al., 2017). In split-belt walking, people do not  
66 adapt their step lengths back to baseline when the speeds of the two belts are changed

67 gradually (Roemmich and Bastian, 2015). However, in all of these tasks, the nervous  
68 system can and does adapt when certain modifications are made to the novel situations  
69 (Krakauer et al., 2019; Selinger et al., 2015; Torres-Oviedo et al., 2011; Wolpert and  
70 Flanagan, 2016; Zhang et al., 2017). This suggests that the nervous system relies on  
71 particular features of the novel situations to determine if and when to initiate adaptation.

72  
73 One potential feature used by the nervous system to initiate adaptation is salient cost  
74 savings. Here we use *cost savings* to refer to an improvement in the nervous system's  
75 objective function. This may be decreased energetic cost, increased stability, increased  
76 accuracy, or some combination of these and other contributors to the objective function.  
77 *Saliency* refers to how clear it is to the nervous system that cost savings can be gained, and  
78 how it should adapt its control policy to gain the savings. As illustrated in Figure 1, saliency  
79 depends on at least three factors. First, execution variability about the nominal policy—due  
80 to either imperfect execution, purposeful exploration, or guidance by an external input—  
81 allows the nervous system to experience a greater range of cost savings if they exist (Figure  
82 1B). Second, measurement noise decreases the ability of the nervous system to discern the  
83 presence of cost savings (Figure 1C). Third, for any given execution variability and  
84 measurement noise, an increase in the gradient of the cost landscape increases the ability  
85 of the nervous system to discern a cost savings (Figure 1D). If cost savings are not salient—  
86 be it due to any combination of shallow cost gradient, high measurement noise, or low  
87 execution variability—the nervous system may choose to exploit its current control policy  
88 because whether it should adapt, and if so how it should adapt, is simply not clear.

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**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 grey 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.

105 Recent studies in walking support the premise that the nervous system relies on salient  
106 cost savings to initiate adaptation. One of the primary real-time objectives of the nervous  
107 system during walking is to minimize energetic cost (Abram et al., 2019; Selinger et al.,  
108 2019, 2015; Simha et al., 2019). In one of our recent studies, we used robotic exoskeletons  
109 to reshape the energetic cost landscape of treadmill walking. Here *cost landscape* refers to  
110 the relationship between step frequency and metabolic energetic cost. We reshaped the  
111 cost landscape to shift the optimal step frequency to step frequencies lower than normally  
112 preferred. Upon their first experience with the new cost landscape, only some participants  
113 spontaneously initiated adaptation to the new optimal step frequency. These *spontaneous*  
114 *initiators* had greater step frequency variability than the *non-spontaneous initiators* who  
115 persisted walking at the previous optimal step frequency. This suggests that the naturally  
116 higher variability increased the saliency of the cost savings to the nervous system which  
117 led to the initiation of adaptation. We were also able to prompt the non-spontaneous  
118 initiators to initiate adaptation by providing them with experience with step frequencies  
119 that resulted in a lower energetic cost. One interpretation of this result is that the  
120 experience increased the saliency of the energetic cost savings for the nervous system  
121 causing it to initiate further exploration. Counter to these findings, we did not find that  
122 increased gait variability was sufficient to initiate adaptation in a subsequent study on over  
123 ground walking (Wong et al., 2019). When compared to our treadmill studies, changes in  
124 cost in this over ground study were due not only to changes in step frequency, but also  
125 speed and terrain. We suspect that the nervous system did not initiate adaptation within  
126 the duration of this over ground experiment because the added dimensionality increased  
127 the complexity of the credit assignment problem making it difficult for the nervous system  
128 to determine which energetic changes could be attributed to its control, and which were  
129 due to the differences in terrain.

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131 In the present study, we aimed to test whether the saliency of energetic cost savings is a  
132 feature that the nervous system uses to initiate adaptation in human walking. To  
133 accomplish this, rather than manipulate measurement noise or movement variability, we  
134 changed saliency by manipulating the gradient of the energetic cost landscape. We  
135 manipulated the gradient using a mechatronic system that applied controlled fore-aft

136 forces to the waist of participants as they walked on a treadmill. These applied forces were  
137 a function of participants' step frequency and acted to increase energetic cost at high step  
138 frequencies and reduce it at low step frequencies. By making the forces a function of only  
139 step frequency and keeping the walking speed constant, we aimed to only affect the  
140 gradient of the step frequency cost landscape, indirectly signaling to the nervous system  
141 how it should adapt its control policy to obtain cost savings. We increased the gradient of  
142 the cost landscape about participants' originally preferred step frequency by increasing the  
143 magnitude of force change that the system provided for a given change in step frequency.  
144 We hypothesized that increasing the gradient of the cost landscape will cause participants  
145 to spontaneously initiate adaptation of their step frequency.

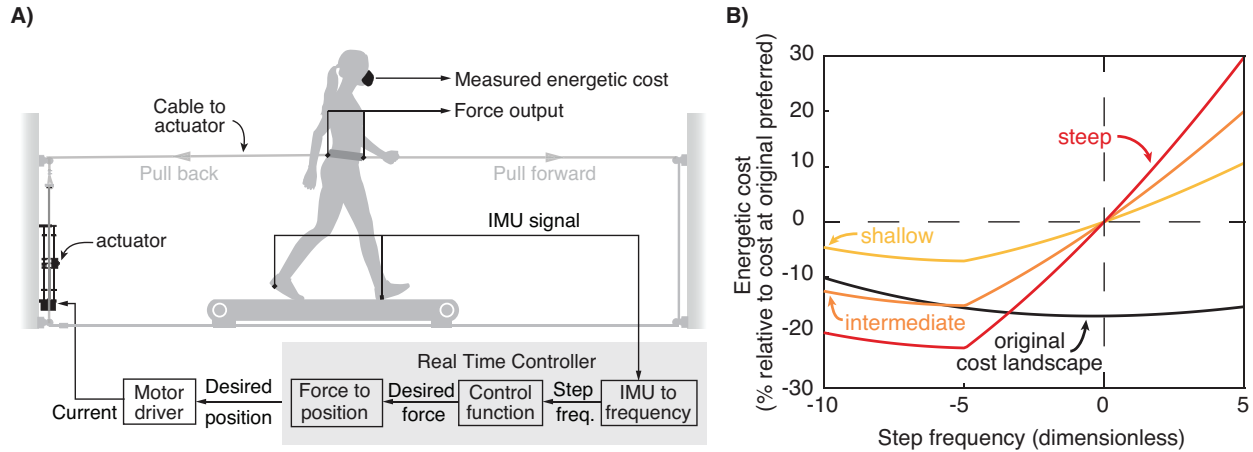
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## 147 **Methods**

### 148 **Experimental design:**

149 We manipulated cost landscapes using our recently developed mechatronic system (Figure  
150 2A). We describe this system in detail in our earlier paper (Simha et al., 2019). Briefly, it  
151 manipulates a participant's original cost landscape by applying fore-aft forces to their waist  
152 while they walk on a treadmill. The controller specifies the forces as a function of the  
153 participant's step frequency. Backward forces increase the energetic cost associated with  
154 the executed step frequency, relative to normal, while moderate forward forces decrease  
155 the energetic cost (Gottschall and Kram, 2003). The system uses inertial measurement  
156 units placed on participants' feet to detect ground contact events, and this signal is  
157 processed by a real-time controller to determine the participants' executed *step frequency*,  
158 defined as the inverse of the time elapsed between left and right foot ground contact  
159 events. We provide the controller with a *control function* that defines the relationship it has  
160 to maintain between the measured step frequency and the applied force. Based on this  
161 control function and the measured step frequency, the controller commands the required  
162 force for each new step to an actuator via a motor driver. The force applied by the actuator  
163 is transmitted to the participants through long tensioned cables that are attached to a hip  
164 belt, and we monitor that force using force transducers in-line with the front and back  
165 cables.

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167  
 168 **Figure 2: A)** Participants walked in a mechatronic system that applied controlled fore-aft forces as a function  
 169 of their walking step frequency. Backward forces provided an energetic penalty, raising the cost of walking  
 170 relative to normal. Moderate forward forces provided an energetic reward, lowering energetic cost. **B)** Using  
 171 simulations, we predicted that participants would experience cost landscapes with gradients of 1.4 (shallow),  
 172 2.8 (intermediate), and 4.2 (steep) percentage change in cost per unit change in step frequency, about their  
 173 originally preferred step frequency (0).

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 175 We tested participants' behavior in cost landscapes of three different gradients (Fig 2B).  
 176 Using data from literature, we can predict for an average participant the energetic cost  
 177 associated with each step frequency when walking without any external force (Umberger  
 178 and Martin, 2007), as well as the energetic cost of walking when a range of fore-aft forces  
 179 are applied but at a fixed step frequency (Gottschall and Kram, 2003). We combined these  
 180 relationships and used them to design three control functions—*shallow*, *intermediate*, and  
 181 *steep*—that created cost landscapes of three different gradients.

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

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 185 
$$F_{intermediate} = \begin{cases} -0.07 \cdot sf - 0.40, & sf \leq -5 \\ -0.39 \cdot sf - 1.98, & sf > -5 \end{cases} \quad (2)$$

186  
 187 
$$F_{steep} = \begin{cases} -0.07 \cdot sf + 0.56, & sf \leq -5 \\ -0.58 \cdot sf - 1.98, & sf > -5 \end{cases} \quad (3)$$

188

189 Here,  $sf$  is a normalized step frequency and is dimensionless. To perform this  
190 normalization, we first measured the average step frequency originally preferred by each  
191 participant during a baseline trial (c.f. Experimental Protocol), as well as the standard  
192 deviation in step frequency about this average preferred step frequency. We then  
193 calculated the normalized step frequency for each step in the subsequent trials by  
194 subtracting the average originally preferred step frequency from each step's measured step  
195 frequency and then dividing by the standard deviation about the originally preferred step  
196 frequency. This normalization controls for the differences between participants in their  
197 step frequency variability, which is normally one of the contributors to the saliency of cost  
198 savings. It also forces measured step frequencies that are equal to the originally preferred  
199 step frequency to evaluate to 0. We normalized the forces applied to a participant by their  
200 body weight. In equations 1-3, the intercepts, slopes, and the forces all have units of  
201 percent body weight ( $sf$  is dimensionless). We designed these control functions to  
202 generate new cost landscapes with cost gradients of 1.4, 2.8, and 4.2 about the originally  
203 preferred step frequency. These gradients have units of percent change in energetic cost  
204 for a unit change in normalized step frequency. For example, were a participant walking in  
205 the intermediate gradient condition to choose a step frequency 1 normalized unit lower  
206 than their originally preferred step frequency, the participant will experience a 2.8%  
207 reduction in energetic cost relative to what they experienced at the originally preferred  
208 step frequency. For comparison, the cost landscape used in Selinger's study roughly  
209 corresponds to the shallowest gradient we use here (Selinger et al., 2019, 2015). To  
210 experience a cost gradient as steep as our steepest, one would have to walk at a step  
211 frequency roughly 7.5% higher than their preferred step frequency in their original cost  
212 landscape (Umberger and Martin, 2007). Finally, we designed all the new cost landscapes  
213 to have the same cost at the originally preferred step frequency. This helped ensure that  
214 when we changed the cost landscape, participants only experienced the gradient change,  
215 without experiencing any change in the average steady-state cost. Since different nervous  
216 systems can respond differently to our control functions, each participant may not  
217 experience exactly the cost landscape that we aimed to create. However, our prior results  
218 show that, on average, we are able to accurately create our designed cost landscapes  
219 (Simha et al., 2019).

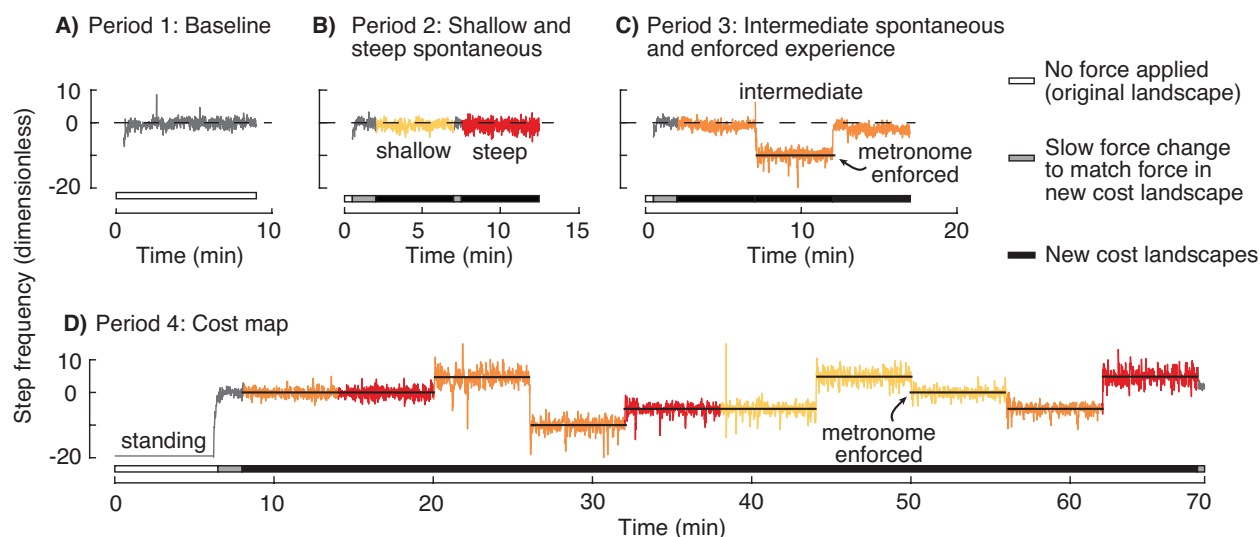


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**Experimental protocol:**

We collected data from 11 participants (mean±SD; Age: 24±3 years; Height: 167±11 cm; Mass: 68±11 kg; Gender: 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 determine the sample size necessary to evaluate our hypothesis, we first performed pilot experiments and estimated that we can expect a group standard deviation of 1.01 steps per minute. We then performed a power analysis for a one-tailed Students' t-test to detect an average change of 1 normalized unit in step frequency ( $\alpha = 0.05$ ,  $1-\beta = 0.90$ ).

Each participant completed four periods of walking on the same day (Figure 3). Prior to the beginning of these four experimental periods, all participants spent ~10 minutes habituating to walking on our treadmill at a speed of 1.25 m·s<sup>-1</sup>. 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 minutes 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 (Figure 3A). We calculated the average and standard deviation of their step frequency from the 6<sup>th</sup> to 9<sup>th</sup> minute 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*.



245  
246 **Figure 3:** Step frequency measured from a representative participant during the different walking periods.  
247 Each participant completed four periods of walking in a single day. **A)** First, they walked for 9 minutes as the  
248 system controlled for a force of 0 N to be applied to their waist. We used this baseline period to estimate their  
249 average original preferred step frequency and original step frequency variability. **B)** Then participants  
250 walked for 5 minutes each in the shallow and steep gradients to test for spontaneous adaptation. **C)** In the  
251 third period, participants walked in an intermediate gradient. We used this condition to test for both  
252 spontaneous adaptation to an intermediate gradient and adaptation after enforced experience with a low  
253 cost. **D)** Finally, we measured the actual gradients experienced by participants in each the cost landscapes.

254  
255 In the second period, we tested whether participants would spontaneously initiate  
256 adaptation in the shallow and steep gradients (Figure 3B). They experienced 0 N for the  
257 first 30 s to allow them to reach a steady-state step frequency (Pagliara et al., 2014). We  
258 programmed the system to ramp up the force over the next minute (minute 0.5 to 1.5) to  
259 the force that would be applied at the participants' originally preferred step frequency in  
260 the new cost landscapes. This ensured that participants were not perturbed by a sudden  
261 change in force when the cost landscape changed. This force was held constant for 30 s  
262 (minute 1.5 to 2; *shallow pre-spontaneous*). The controller then engaged the control  
263 function for the shallow gradient, and participants walked at a self-selected step frequency  
264 for 5 minutes (minute 2 to 7; *shallow spontaneous*). Then the controller switched to the  
265 steep gradient. Once again, we ensured that participants were not perturbed during the  
266 cost landscape transition by using a limit on the rate at which the force could change for 30  
267 s (minute 7 to 7.5). Participants then self-selected their step frequency for five minutes

268 (minute 7.5 to 12.5; *steep spontaneous*). To avoid fatigue, we then provided a break of 5-10  
269 minutes before beginning the third period. For each participant, we averaged their self-  
270 selected step frequency over the last 30 s of walking in each gradient to determine their  
271 *spontaneous adaptation* in that gradient (*shallow spontaneous*: minute 6.5 to 7; *steep*  
272 *spontaneous*: minute 12 to 12.5).

273

274 We used the third period to test for adaptation in an intermediate gradient (Figure 3C). The  
275 first part of this period served as a sort of Goldilocks test in the event that the shallow and  
276 steep gradients were both perceived as extreme by the nervous system (Kidd et al., 2012).  
277 Similar to the second period, the force was ramped up in the first two minutes to prevent  
278 perturbing forces. The controller then engaged the control function for the intermediate  
279 gradient, and participants self-selected their step frequency for 5 minutes (minute 2 to 7;  
280 *intermediate spontaneous*). One possible outcome of our experiment was that participants  
281 would not spontaneously adapt in any of the gradients. With this outcome, we would not be  
282 able to distinguish between the possibility that participants will adapt but not  
283 spontaneously, and the possibility that participants won't adapt at all in our system with  
284 our experimental paradigm. Therefore, the next part of this experimental period was to  
285 verify whether adaptation was possible at all. Prior work has shown that experiencing a  
286 lower cost in a new cost landscape is sufficient to cause the nervous system to initiate  
287 adaptation (Selinger et al., 2019). Using this principle, we next required participants to  
288 match their step frequency to an audio metronome that played a frequency -10 normalized  
289 units away from their originally preferred step frequency. According to our designed cost  
290 landscape, we expected this step frequency to provide a cost savings of 12.5% relative to  
291 the cost at 0. After five minutes of matching the metronome (minute 7 to 12; *intermediate*  
292 *metronome guided*), the metronome was turned off and participants self-selected their step  
293 frequency for another five minutes (minute 12 to 17; *intermediate post-experience*). Once  
294 again, we averaged each participant's step frequency during the last 30 s of each condition  
295 to determine their preferred step frequency in that condition (*intermediate spontaneous*:  
296 minute 6.5 to 7; *intermediate post-experience*: minute 16.5 to 17).

297

298 The purpose of the fourth period was to measure the actual energetic cost experienced by  
299 the participants in each of the new cost landscapes (*cost mapping*; Figure 3D). During this  
300 period, participants were also instrumented with a respiratory gas analysis system (Vmax  
301 Encore Metabolic Cart, Viasys, Pennsylvania, USA). They spent the first six minutes  
302 standing still while we measured their resting metabolic rate (minute 0 to 6). They then  
303 started walking while the mechatronic system maintained a force of 0 N to allow them to  
304 reach a steady-state gait (minute 6 to 7). Following this, participants walked at specific  
305 walking conditions chosen to allow us to estimate the gradient about the originally  
306 preferred step frequency in each of the cost landscapes, and also to estimate if the  
307 *experience low* period indeed allowed participants to experience a lower cost. Participants  
308 walked in 10 conditions total: step frequencies of 0, -5, and +5 in shallow, intermediate and  
309 steep gradients, and -10 in only the intermediate gradient. We enforced this by instructing  
310 participants to match an audio metronome that played these frequencies. We programmed  
311 the controller to present these conditions in a random order to each participant, to prevent  
312 any order effects on these metabolic energy measures. To determine energetic cost, we  
313 measured the total volume of oxygen consumed and volume of carbon dioxide produced in  
314 the last three minutes of each condition, and divided them by the duration over which they  
315 were measured, to obtain the steady state average rates of oxygen consumption ( $\dot{V}_{O_2}$ ) and  
316 carbon dioxide production ( $\dot{V}_{CO_2}$ ). We then estimated the metabolic rate using the following  
317 equation (Adamczyk et al., 2006; Brockway, 1987; Weir, 1949):

$$318 \quad P_{met,gross} = (16.48 \frac{W s}{ml O_2} \dot{V}_{O_2}) + (4.48 \frac{W s}{ml CO_2} \dot{V}_{CO_2}) \quad (4)$$

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

322

### 323 **Data analysis:**

324 We first determined the average gradients and metronome-guided cost that participants  
325 experienced in each cost landscape. We used MATLAB's fitlm command to find the best  
326 linear fit through the energetic costs at -5, 0, +5 normalized step frequencies for each  
327 participant, in each cost landscape. We define the cost landscape gradient for each

328 participant as the slope of this fit. We also used a one-tailed paired Students' t-test to  
329 determine whether the cost at a step frequency of  $-10$ , where we held participants during  
330 the *intermediate metronome guided* condition, is lower than the cost at a step frequency of  
331 0 in the intermediate gradient.

332  
333 We evaluated whether participants spontaneously initiated adaptation in response to  
334 steeper gradients. We first compared the preferred step frequency in the shallow gradient  
335 with the originally preferred step frequency using a one-tailed Student's t-test. We found  
336 that these values were indeed different, but we did not attribute this shift in preferred step  
337 frequency to an adaptation in response to a new cost gradient (c.f. Results). To determine if  
338 there was any additional changes in preferred step frequency in the steeper gradients, we  
339 then compared the average step frequencies during the spontaneous adaptation periods in  
340 the intermediate and steep gradient to the same period in the shallow gradient.

341  
342 We also determined whether participants initiated adaptation after enforced experience  
343 with a low cost. We used a one-tailed paired Students t-test to determine whether  
344 participants' preferred step frequency after the *intermediate metronome guided* condition  
345 was significantly lower than the average step frequency 30 s prior to the experience with  
346 low cost. The step frequency in this 30s prior to the experience corresponds to the  
347 spontaneous adaptation in the intermediate gradient, allowing us to determine whether  
348 the metronome guided experience generated adaptation that did not occur spontaneously.

349  
350 In the conditions where we observed adaptation, we characterized the rate of adaptation.  
351 We did so because a preferred step frequency can arise from fast predictive processes that  
352 can occur over a few seconds or optimization processes that can occur over tens or  
353 hundreds of seconds (Pagliara et al., 2014). As described in the introduction, we are  
354 interested in the slow process since it is indicative of the nervous system learning to adapt  
355 its policy to a novel situation. We modelled each participant's adaptation of step frequency  
356 over time as a two-process exponential. We first averaged the step frequency during the  
357 last 30 s prior to the beginning of the condition of interest, and the step frequency during  
358 the last 30 s of the condition. If these two averages were different, we normalized the step

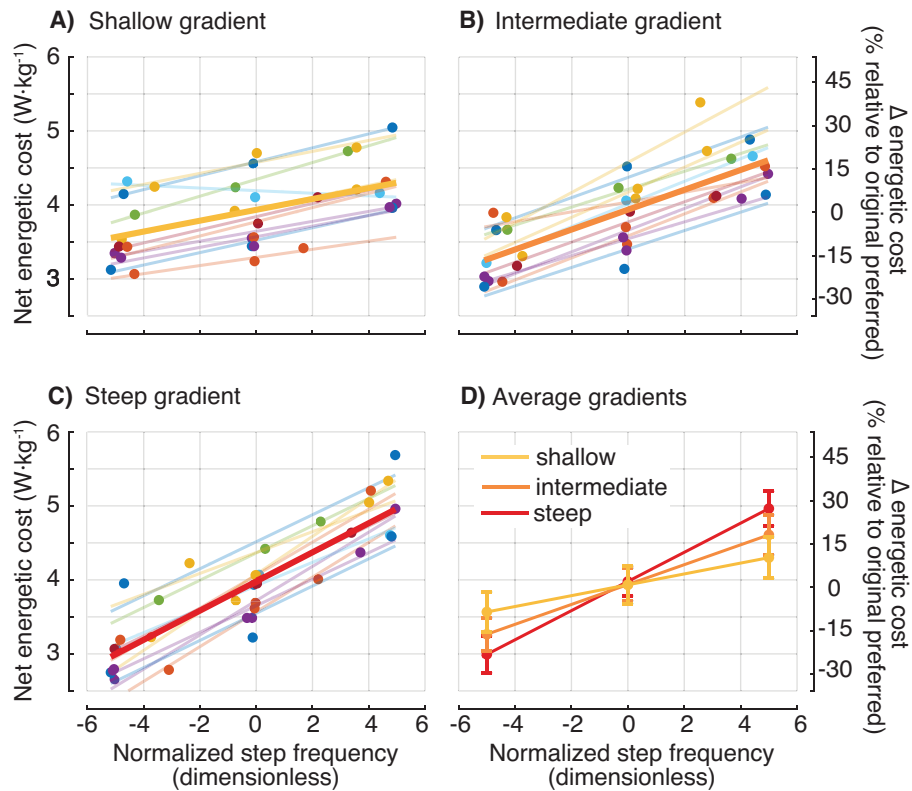
359 frequency data during that condition such that the average step frequency of the 30 s prior  
360 to the condition evaluated to 0, and the average of the last 30 s evaluated to 1. We then  
361 used least squares regression implemented through MATLAB's fitnlm function to model  
362 these data as the sum of two exponentials (Pagliara et al., 2014). We used the time  
363 constants from this model to estimate the duration of the optimization process.

364

## 365 **Results**

366 We were successful in creating cost landscapes of different gradients. We found that  
367 participants on average experienced a shallow gradient of  $0.07 \pm 0.03 \text{ W} \cdot \text{kg}^{-1}$  (mean $\pm$ SD), an  
368 intermediate gradient of  $0.14 \pm 0.03 \text{ W} \cdot \text{kg}^{-1}$ , and a steep gradient of  $0.20 \pm 0.04 \text{ W} \cdot \text{kg}^{-1}$   
369 (Figure 4). This is calculated as the change in energetic cost per normalized unit of step  
370 frequency. We use 1 standard deviation of participants' preferred step frequency in their  
371 original cost landscape, to normalize the measured step frequency. This means that  
372 participants experience the reported gradient through a variability of 0.5 standard  
373 deviations higher and lower than their originally preferred step frequency. Thus, 1  
374 standard deviation higher and lower than their originally preferred step frequency, which  
375 accounts for 68% of their steps, would have allowed participants to experience a change in  
376 energetic cost of 3.6%, 7.2%, and 10.2% in the shallow, intermediate, and steep gradients,  
377 respectively. We also found that when participants in the intermediate gradient were held -  
378 10 normalized step frequencies lower than their originally preferred step frequency, they  
379 experienced an average cost savings of  $8.1\% \pm 9.1\%$  relative to the cost at the originally  
380 preferred step frequency ( $p=0.006$ ).

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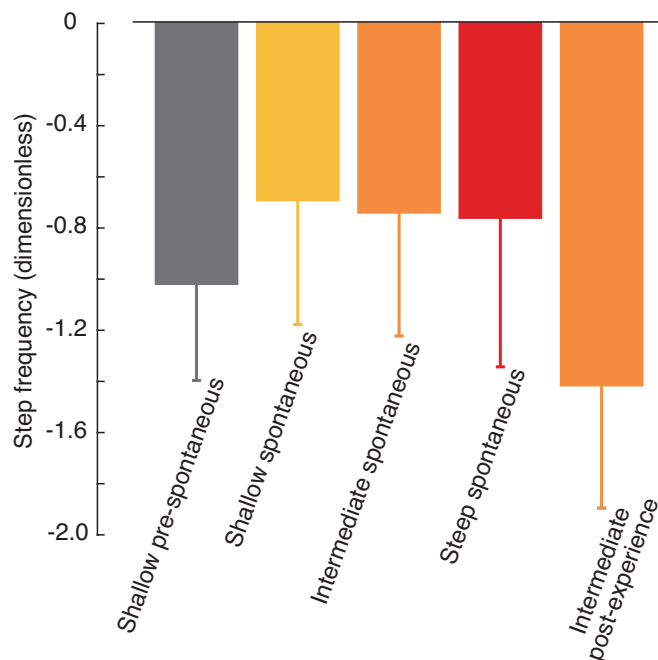
383 **Figure 4: A)** Shallow **B)** intermediate and **C)** steep gradients. Each filled circle represents one measurement  
384 from one participant. Light lines are linear fits to each participant's cost measurements. Data points and best-  
385 fit lines from a given participant is presented in a single colour. Thick lines are the average of these linear fits.  
386 **D)** On average the gradients are increasing from shallow to steep. The filled circles represent the average cost  
387 measures at the commanded step frequencies, and the error bars represent the 95% CI of the same.

388 Participants did not spontaneously initiate adaptation in response to steeper cost  
389 gradients. In the second period, participants first experienced the shallow cost landscape,  
390 and then the steep cost landscape. They walked freely at their self-selected step frequency  
391 for 5 min in both cost landscapes. The average step frequency from the last 30 seconds of  
392 the shallow period was lower than the original preferred step frequency ( $-0.69 \pm 0.82$  vs. 0;  
393  $p = 0.01$ ). However, this step frequency was indistinguishable from the average step  
394 frequency preferred by participants during the 30 s prior to the beginning of the shallow  
395 gradient (Figure 5: Shallow pre-spontaneous vs Shallow spontaneous;  $-0.69 \pm 0.82$  vs. -  
396  $1.02 \pm 0.64$ ;  $p = 0.33$ ). Therefore, we do not interpret this to be an initiation of adaptation  
397 towards the optimal policy. When the system switched from the shallow landscape to the  
398 steep landscape, participants still did not initiate adaptation, and preferred a step

399 frequency (Figure 5: Steep spontaneous;  $-0.76 \pm 0.99$ ) that was indistinguishable from that  
400 preferred in the shallow cost landscape (Figure 5: Shallow spontaneous;  $-0.69 \pm 0.82$ ;  $p =$   
401  $0.40$ ). Our goldilocks test with the intermediate gradient also resulted in preferred step  
402 frequencies that were indistinguishable from that preferred in the shallow landscape  
403 (Figure 5: Shallow spontaneous vs Intermediate spontaneous;  $-0.69 \pm 0.82$  vs.  $-0.74 \pm 0.82$ ;  $p$   
404  $= 0.43$ ).

405  
406 Participants did, however, initiate adaptation after enforced experience with a lower cost.  
407 We allowed participants to self-select their step frequency after matching a metronome  
408 that held them at a step frequency that had a cost lower than the cost at 0 in the  
409 intermediate cost landscape. On average, participants adapted by  $-1.41 \pm 0.81$  towards the  
410 new cost minimum (Figure 5: Intermediate post-experience). This adaptation was to step  
411 frequencies significantly lower than that spontaneously preferred in the intermediate  
412 gradient ( $p=0.007$ ). It led to an average cost savings of  $4.80 \pm 3.12\%$  relative to the cost at 0.  
413 We found that the time course of the change in step frequency of most participants was  
414 captured well with a two-process exponential model ( $RMSE=0.16 \pm 0.08$ ;  $R$ -  
415  $squared=0.36 \pm 0.21$ ). The time constant of the fast process was  $4.4 \pm 2.5$  s while that of the  
416 slow process was  $190.2 \pm 209$  s. We interpret the presence of this slow process as evidence  
417 that the nervous system indeed initiated adaptation in response to the enforced experience  
418 with a lower cost gait.





419  
420 **Figure 5:** Average spontaneous adaptation in the shallow gradient was indistinguishable from participants'  
421 preferred step frequency just prior to the beginning of the shallow cost landscape (shallow pre-spontaneous  
422 vs shallow spontaneous). The spontaneous adaptation in all gradients were also indistinguishable from each  
423 other after five minutes of walking (shallow, intermediate, steep spontaneous). However, after experience  
424 with a lower cost in the intermediate gradient, participants preferred to walk at a significantly lower step  
425 frequency (intermediate post-experience).

## 426 **Discussion**

427 Contrary to our hypothesis, steeper gradients did not lead to spontaneous initiation of  
428 adaptation. This null finding is not because our methods were unsuccessful in creating  
429 gradients of increasing steepness. We used our cost mapping trials to verify that the  
430 participants did indeed experience three different gradients—the intermediate and steep  
431 gradients were about 2-fold and 3-fold the shallow gradient, respectively. The lack of  
432 initiation also does not appear to be a consequence of the rapid exposure to multiple  
433 gradient conditions preventing the nervous system from attempting any adaptation. We  
434 verified this by leveraging results from previous studies that found that adaptation can be  
435 initiated by guiding the nervous system to experience a cost lower than the cost at the  
436 originally preferred step frequency (Selinger et al., 2019). We did the same here and found  
437 that participants could indeed initiate adaptation in the intermediate landscape after such  
438 experience, despite the intermediate landscape being the third landscape experienced by

439 participants. When considered together, these results suggest that either the nervous  
440 system does not use salient cost savings to initiate adaptation, or that the cost savings were  
441 not salient to the nervous system in our experiment.

442  
443 For savings to be salient, the nervous system needs to both detect that cost savings can be  
444 gained and determine how it should adapt its control policy to gain the savings. Depending  
445 upon how the nervous system senses energetic cost, it may be challenging for the nervous  
446 system to detect cost savings from the cost landscape gradient. For example, one possible  
447 candidate sensory system for estimating energetic cost involves the ergoreceptors that are  
448 sensitive to the slow build-up, or slow reduction, of muscle metabolic byproducts (Amann  
449 et al., 2011; Iwamoto et al., 1985; Mitchell et al., 1983). This build-up creates a sensory  
450 response that is an integration of the effect of many steps, rather than one that closely  
451 follows the step-to-step changes in energetic cost. It will be more difficult for the nervous  
452 system to detect a gradient in cost landscape from the step-to-step variability in energetic  
453 cost when using this mechanism because integration has the effect of decreasing the sensed  
454 gradient, perhaps even to zero if the build-up is particularly slow. This, or a similar  
455 integrative sensing mechanism, may be why metronome-guided experience is effective at  
456 initiating adaptation—the metronome holds participants at a lower cost for many steps  
457 allowing time for integration. However, some participants in some conditions are able to  
458 use the step-to-step variability in energetic cost to spontaneously initiate adaptation  
459 (Selinger et al., 2019). This suggests that if a slow sensing system does indeed play a role in  
460 estimating energetic cost, it is not the only contributing system.

461  
462 Another possibility for the lack of initiation of adaptation is that the gradients allowed  
463 participants' nervous systems to sense the presence of cost savings but not how to adapt  
464 their control policy to obtain those savings. That is, the nervous system has difficulty with  
465 credit assignment in our experiment (Guerguiev et al., 2020). We manipulated the cost  
466 gradient associated with only one gait parameter—step frequency—to allow the nervous  
467 system to detect an increase in cost savings and detect the gait parameter to adapt to  
468 obtain those savings. But when walking in our system, we suspect that it is not clear to  
469 most participants that the backward force depends on any aspect of their gait, including

470 their step frequency. It appears to be challenging for the nervous system to identify salient  
471 cost savings using the structure of natural variability in gait to determine the gradient of a  
472 cost landscape—a finding consistent with our earlier experiment studying adaptation in  
473 over ground walking (Wong et al., 2019). Metronome-guided experience of step  
474 frequencies with lower cost may provide the nervous system with an explicit association  
475 between the cost savings and the changes to control policy that provide those cost savings.  
476 Similarly, reaching experiments have found that presenting participants with multiple  
477 different force-fields interferes with learning, but that such interference can be overcome  
478 with certain contextual cues such as follow through movements or cues that associate a  
479 change in the optimal control policy with another change such as spatial location of  
480 movement (Howard et al., 2015, 2013). Differences in contextual clues might explain why it  
481 was easier for the nervous system to identify that there was a relationship between step  
482 frequency and the changes to knee torque for some participants in our previous  
483 experiment than with step frequency and torso forces in the present experiment (Selinger  
484 et al., 2019). This interpretation is consistent with recent study in visuomotor adaptation  
485 that found that implicit and explicit learning work together to improve adaptation  
486 (Miyamoto et al., 2020).

487  
488 While we designed our custom-built equipment and our protocol to meet the requirement  
489 for energetic cost saliency, our experiment nevertheless had limitations. Towards this  
490 requirement, the maximum cost savings that participants experienced from their  
491 variability in step frequency, relative to the cost at their originally preferred step  
492 frequency, was 5.1% in the steep gradient. In contrast, participants experienced cost  
493 savings of 8.2% during their metronome-guided lower cost experience in the intermediate  
494 gradient. This suggests that even the steep gradient may not have allowed participants to  
495 experience a large enough cost savings. However, we suspect this is not the case because in  
496 our previous study with the shallow gradient, participants initiated adaptation after  
497 experiencing cost savings of only 3.5% through similar metronome-guided walking (Simha  
498 et al., 2019). This earlier cost savings was smaller than that experienced by our current  
499 participants in the steep gradient condition suggesting that the currently experienced cost

500 savings, at least in the steep gradient condition, were sufficiently large for the nervous  
501 system to detect.

502

503 A second limitation is that our experimental design resulted in participants preferring step  
504 frequencies slightly lower than the original preferred step frequencies in all gradient  
505 conditions (Figure 5). We do not interpret these shifts as evidence of the initiation of  
506 energetic cost optimization in response to new cost landscapes. Our rationale is that  
507 participants were already walking at shifted step frequency during the 30 s prior to the  
508 beginning of each new cost landscape (shallow:  $-1.02 \pm 0.64$ , intermediate:  $-0.74 \pm 0.82$ ,  
509 steep:  $-0.62 \pm 0.54$ ). Why is step frequency shifted lower than the baseline measures both  
510 before and during the experience with the new cost landscapes? One possible explanation  
511 is that we may not have provided a long enough baseline period for participants to settle  
512 into their preferred step frequency. However, others have found that two minutes of  
513 walking is sufficient for stride frequency to reach steady state—we provided 9 minutes  
514 (Van de Putte et al., 2006; Wall and Charteris, 1981). A second possible explanation for the  
515 presence of these shifts may be the net backward force that participants experienced both  
516 immediately before and during the cost landscape, but not during the baseline phase when  
517 the net force was zero. Our system slowly ramped up the backward force to that which  
518 participants would experience in the new cost landscapes at their originally preferred step  
519 frequency. The force was then held constant for 30 s before the controller switched to the  
520 new cost landscapes, and our step frequency estimate prior to the beginning of the new  
521 cost landscape is from this constant-force period. However, concerned about the possible  
522 role of net backward force on step frequency, we performed pilot experiments prior to our  
523 reported experiments and found no relationship. In support of our pilot results, a recent  
524 study also found that backward forces do not have an effect on stride period (Dewolf et al.,  
525 2020). Furthermore, walking uphill, which is biomechanically similar to experiencing a net  
526 backward force, also results in step frequencies that are not significantly different from  
527 walking on level (Ortega and Farley, 2015). Further research will be required to  
528 understand why we observed this consistent shift in step frequency.

529

530 After metronome-guided experience, our participants did not converge on the energy  
531 minimal step frequency. To determine the location of the cost minimum, and the magnitude  
532 of cost savings obtainable at the minimum, we fit a quadratic relationship to the costs  
533 measured in the intermediate gradient condition during cost mapping. From this  
534 relationship, we estimate that, on average, participants could have obtained a cost savings  
535 of 10.8% if they had shifted their step frequency  $-6.1$  normalized units away from their  
536 originally preferred step frequency. Yet we found that participants only adapted their step  
537 frequency by  $-1.4 \pm 0.8$  to obtain a cost savings of only  $4.83 \pm 3.61\%$ . This might suggest to  
538 some that energetic cost savings do not play a role in the adaptation of step frequency in  
539 the cost landscapes we used. We suspect that this is not the case since participants did  
540 adapt after experience with a lower energetic cost. A candidate explanation is that the  
541 nervous system seeks to minimize an objective function that is a combination of energetic  
542 cost, stability, accuracy and other contributors (Abram et al., 2019). The minimum of this  
543 combined cost function may coincide with the final preferred step frequency and not with  
544 the energetic cost minimum.

545  
546 In conclusion, the nervous system does not solely rely on the gradient of energetic cost to  
547 initiate adaptation in novel situations. As we and others have previously found, explicit  
548 experience with more optimal movements can assist with the initiation of adaptation. A  
549 better understanding of the interplay between implicit and explicit experience for the  
550 nervous system to initiate adaptation when the saliency of cost savings is not apparent may  
551 help improve rehabilitation for those recovering from injuries, help coaches speed up  
552 training with new techniques, or aid scientists looking to study adaptation in complex  
553 novel environments.

554

555

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