

Humans Can Continuously Optimize Energetic Cost during Walking

Highlights

- People readily adapt established gait patterns to minimize energy use
- People converge on new energetic optima within minutes, even for small cost savings
- Updated predictions about energetically optimal gaits allow re-convergence within seconds
- Energetic cost is not just an outcome of movement, but also continuously shapes it

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In Brief

Selinger et al. provide a physiological basis for our inherent “laziness.” Using robotic exoskeletons to manipulate the most efficient way to walk, the authors made abnormal ways of walking energetically optimal. They found that their subjects swiftly discovered these gaits and learned to predict them, even when the energetic benefits were small.

Humans Can Continuously Optimize Energetic Cost during Walking

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SUMMARY

People prefer to move in ways that minimize their energetic cost [1–9]. For example, people tend to walk at a speed that minimizes energy use per unit distance [5–8] and, for that speed, they select a step frequency that makes walking less costly [3, 4, 6, 10–12]. Although aspects of this preference appear to be established over both evolutionary [9, 13–15] and developmental [16] timescales, it remains unclear whether people can also optimize energetic cost in real time. Here we show that during walking, people readily adapt established motor programs to minimize energy use. To accomplish this, we used robotic exoskeletons to shift people's energetically optimal step frequency to frequencies higher and lower than normally preferred. In response, we found that subjects adapted their step frequency to converge on the new energetic optima within minutes and in response to relatively small savings in cost (<5%). When transiently perturbed from their new optimal gait, subjects relied on an updated prediction to rapidly re-converge within seconds. Our collective findings indicate that energetic cost is not just an outcome of movement, but also plays a central role in continuously shaping it.

RESULTS

That people prefer to move in energetically optimal ways has been established for decades and now represents a central principle of movement science [1, 17, 18]. But the processes by which people discover their optimal patterns are not clear. Much theorizing has focused on optima being established over evolutionary timescales, through changes to body shape, muscle action, and the hardwiring of neural circuitry [9, 13–15]. Energy optimization may also occur over the course of a lifetime, as years of experience could allow people to learn the optimal way to move in familiar situations and allow training to tune physiology to be more economical [16]. An additional hypothesis—one that underpins many modern theories of motor control—is that people can adjust their movements to continuously optimize energetic cost [15, 19–23]. Only recently has energetic cost been assessed during standard adaptation paradigms, and it was indeed found that cost was lower after adaptation than before in both reaching and walking tasks [23, 24]. These studies, while

tantalizingly suggestive, were not designed to test whether energetic cost minimization was a control objective of the central nervous system, leaving the possibility that the measured reductions in energetic cost were correlated with alternative nervous system goals, such as stability, accuracy, or force minimization [25–28].

Here we directly address the continuous optimization hypothesis using robotic exoskeletons to create novel energetic landscapes and then test whether walking subjects adopt the necessary gait adaptions to find new optima. Of all possible energetic landscapes, we chose to manipulate the relationship between step frequency and energetic cost because step frequency is a fundamental characteristic of gait, people have strong preferences for particular step frequencies, and these preferred frequencies are energetically optimal [10, 11]. We manipulated the relationship using lightweight robotic exoskeletons to apply torques that resisted the motion of the knee joints (Figures 1A and 1B). To shift the energetic optimum to lower step frequencies, we had the exoskeleton controller use a “penalize-high” control function that applied a resistive torque, and therefore an added energetic penalty, that was minimal at low step frequencies and increased as step frequency increased (Figures 1C, 1D and S1). To shift the energetic optimum to higher step frequencies, we used a “penalize-low” control function, in which the slope of the penalty was reversed (Figures 1C, 1D and S1). The control functions were designed to create a clear energetic gradient for step frequencies in the neighborhood of subjects' initial preferred step frequency, yet keep all resistive torques low enough to allow relatively natural gaits. To distinguish between energetic cost optimization and simply minimizing the resistive torque applied to the limb, we also strived to design the control functions such that the energetic cost optima occurred at step frequencies distinct from those that minimized exoskeleton resistive torque. It is not possible to design control functions that specifically rule out all alternative objectives to energetic cost minimization. But to be indistinguishable from energy minimization, optimization of these alternative objectives would need to yield step-frequency adaptations in the same directions, and by about the same magnitudes, as those predicted by our novel energetic landscapes.

Natural Gait Variability Does Not Reliably Initiate Optimization

We first sought to determine whether our subjects would adapt to a new energetically optimal step frequency given limited experience with the novel energetic landscape and without being perturbed away from their natural gait. Subjects were assigned

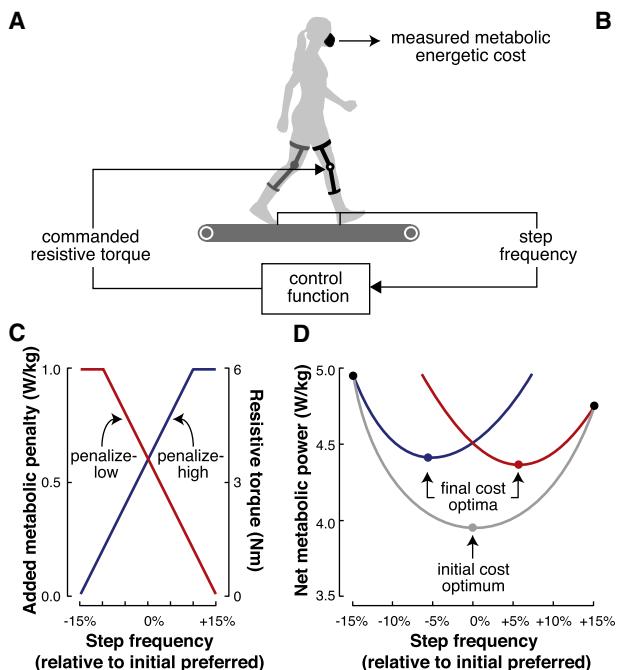


Figure 1. Experimental Design

(A and B) By controlling a motor attached to the gear train of our exoskeletons, we can apply a resistance to the limb that is proportional to the subject's step frequency. (C) Schematic design of the penalize-low (red) and penalize-high (blue) control functions. (D) Schematic energetic landscapes. Addition of the energetic cost of the penalize-low control function to the natural cost curve (gray) produces a cost curve with the optimum shifted to higher step frequencies (red curve). The optimum can instead be shifted to lower step frequencies (blue curve) by addition of the energetic cost of the penalize-high control function to the natural cost curve. See also Figure S1.



to both the penalize-high and penalize-low control functions, in random order, on two separate testing days. On each day, during an initial baseline trial, subjects first walked for 12 min while wearing the exoskeletons, but with the controller turned off (Figure 2A, baseline). This allowed us to determine their “initial preferred step frequency,” which we defined from the final three minutes of walking. All walking took place on an instrumented treadmill (FIT, Bertec Corporation) at 1.25 m/s, and we measured step frequency from treadmill foot contact events. All subjects appeared to settle into a steady-state step frequency within 9 min. On average, subjects walked at 1.8 ± 0.1 Hz (mean \pm SD), and from step to step subjects' step frequency varied about this average by $1.1\% \pm 0.3\%$ (mean \pm SD). We then turned the controller on, resulting in an applied resistive torque that was dependent on step frequency, and the subjects walked for an additional 12 min (Figure 2B, first adaptation). During this time, subjects showed no adaptation in step frequency (penalize-high: $p = 4.3 \times 10^{-1}$; penalize-low: $p = 4.4 \times 10^{-1}$; Figure 3A). They continued to walk at their initial preferred step frequency even though we designed the controller such that minor adjustments to step frequency would result in a more economical gait.

Broad Experience with the Energetic Landscape Initiates Optimization

We next gave our subjects experience with the novel energetic landscape across a wide range of step frequencies and then once again looked for adaptations toward the novel energetic minima. This was accomplished by instructing subjects to self-explore walking with high and low step frequencies, as well as to match their steps to different steady-state and sinusoidally varying metronome tempos (Figure 2C, exploration). After this 15 min exploration period, subjects were again allowed to self-select their step frequency (Figure 2D, second adaptation), and we found that subjects immediately made

large adaptations in step frequency toward the energetic minima (Figure 3A). To robustly determine whether this was a new preferred step frequency, we had subjects match a metronome tempo for 6 min that perturbed them toward both higher resistive torques (penalize-high: +10%; penalize-low: -10%) and lower resistive torques (penalize-high: -10%; penalize-low: +10%) (Figure 2D, second adaptation). After each perturbation, subjects were allowed to self-select their step frequency for another 12 min, and we found that they returned to a step frequency that was shifted toward the energetic optima (Figure 3). We defined the average of the final 3 min of self-selected

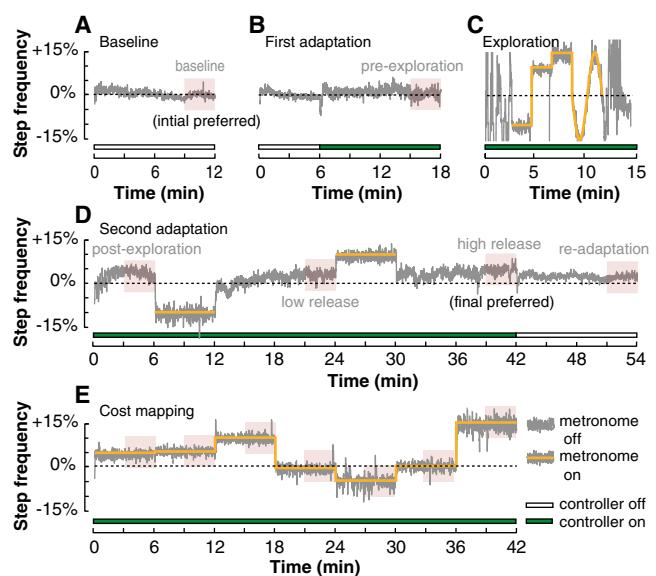


Figure 2. Experimental Protocol

Measured step frequency from a representative subject for a single day of testing with the penalize-low control function. Subjects completed five testing periods: baseline (A), first adaptation (B), exploration (C), second adaptation (D), and cost mapping (E), with a rest period (5–10 min) between each period. For all periods, regions of red shading illustrate the time windows during which we assessed steady-state step frequencies and metabolic costs.

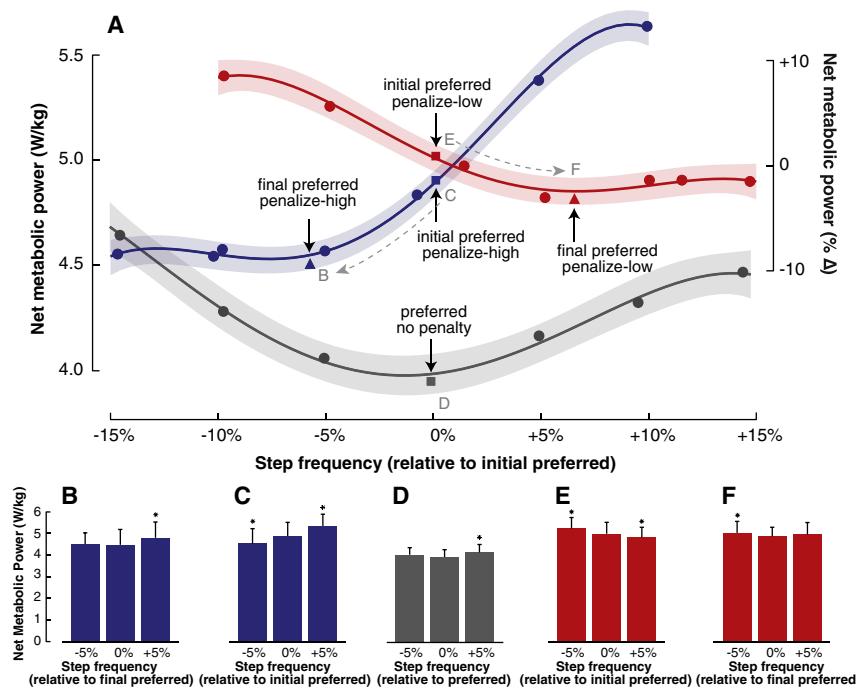


Figure 3. Optimization of Energetic Cost

(A) Energetic landscapes, averaged across all subjects, for the penalize-high (blue) and penalize-low (red) control functions, as well as for the controller off condition (gray). The lines are fourth-order polynomial fits, and the shading shows their 95% confidence intervals, shown only for illustrative purposes. Dashed gray arrows illustrate the directions of adaptation from initial preferred to final preferred step frequencies.

(B–F) Comparisons of energetic costs, averaged across all subjects, around the initial preferred step frequencies (C–E) and final preferred step frequencies (B, D, and F). Error bars represent 1 SD. Asterisks indicate statistically significant differences in energetic cost when compared to the cost at the initial or final preferred step frequency (0%).

step frequency after the last perturbation as the “final preferred step frequency.” On average, when given the penalize-high control function, subjects decreased their step frequency by $5.7\% \pm 3.9\%$ (mean \pm SD), whereas for the penalize-low control function, subjects’ step frequency increased by $6.9\% \pm 4.3\%$. These final preferred step frequencies were distinct from what subjects initially preferred (penalize-high: $p = 1.3 \times 10^{-3}$; penalize-low: $p = 6.2 \times 10^{-4}$), and they were distinct from those that would minimize the resistive torque being applied to the limb (penalize-high: $p = 5.2 \times 10^{-5}$; penalize-low: $p = 2.4 \times 10^{-4}$).

Gait Adaptations Converge on Energetic Optima

We next sought to determine how our subjects’ final preferred step frequency compared to the energetically optimal step frequency by mapping their energetic landscape. We again turned the controller on and had subjects walk to steady-state metronome tempos for 6 min each (Figure 2E, cost mapping), including tempos about the initial preferred step frequency (+5%, 0%, -5%) and about the final preferred step frequency (+5%, 0%, -5%). We measured metabolic energetic cost using respiratory gas analysis equipment (VMax Encore Metabolic Cart, ViaSys). As hypothesized, our subjects had indeed increased or decreased their self-selected step frequency, whichever was required by the new landscape, to converge on the new energetic optima (Figure 4). These adaptations were to achieve relatively small cost savings. The energetic cost at the final preferred step frequency was $8.1\% \pm 7.0\%$ lower than the energetic cost at the initial preferred step frequency for the penalize-high control function ($p = 4.1 \times 10^{-3}$) and $4.0\% \pm 3.8\%$ lower for the penalize-low control function ($p = 9.7 \times 10^{-3}$). Subjects achieved most of the costs savings immediately after the exploration period, yet they continued to fine-tune their step frequency for vanishingly small energetic

cost savings (Figure 3). Evaluation of the energetic cost at the final preferred step frequencies, and at step frequencies on either side of the final values, suggested that subjects converged to, or at least near, their minimum costs; no further

cost savings appear to be gained by additional adjustments to preferred step frequency (Figures 4B and 4F).

Gait Adaptations Use Updated Predictions of Energetically Optimal Gaits

After perturbations using the metronome tempos, our subjects converged toward their new preferred step frequency within seconds (Figures 3B and 3C). In cases where subjects were held at metronome tempos that resulted in high resistive torques (penalize-high: +10%; penalize-low: -10%) and then released, they immediately bypassed their initial preferred step frequency, which was now energetically suboptimal, to quickly converge on the new preferred and energetically optimal step frequency. All subjects bypassed the initial preferred step frequency in less than 10 s. When held at metronome tempos that resulted in low resistive torques (penalize-high: -10%; penalize-low: +10%) and then released, subjects actually elected to increase the resistance on their limb, again within seconds, in order to reach the energetic optima. We have previously argued that the timescale of such rapid adaptations to energetically optimal gaits requires the prediction of energetic cost, rather than its direct optimization [29]. That subjects rapidly converged on new energetic minima indicates that subjects had updated their prediction of the optimal gait for each control function. This was also observable when the high or low penalty was removed for a final 12 min (Figure 2D, second adaptation); subjects’ step frequency remained shifted toward the control function optima for minutes despite a return to the natural energetic landscape and its former energetically minimal gait (Figure 3).

DISCUSSION

Motor variability has traditionally been thought of as an inevitable, if not potentially burdensome, consequence of imperfect

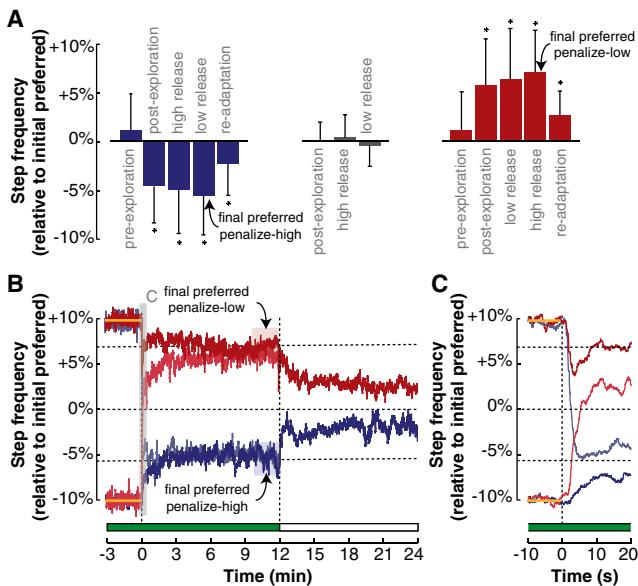


Figure 4. Time Course of Step-Frequency Adaptations

(A) Steady-state step frequencies, averaged across subjects, throughout the course of the protocol. Error bars represent 1 SD. Results for the penalize-high control function are shown in blue, the penalize-low control function in red, and the controller off condition in gray. Asterisks indicate average step frequencies that are statistically different from 0% (the initial preferred step frequency).

(B) Step-frequency time-series data, averaged across subjects, for the release high and low from the second adaptation period. For the penalize-high controller, the release from high and low step frequencies is shown in light and dark blue, respectively. For the penalize-low controller, the release from low and high step frequencies is shown in light and dark red, respectively. The horizontal bar indicates when the controller is turned on (green fill) and off (white fill), and the yellow lines indicate the prescribed metronome frequencies. (C) Average step-frequency time-series data for a 30 s window about the metronome release (at time 0).

neural control. However, recent findings have reframed motor variability as an asset—one that can facilitate and enhance motor learning. For example, songbirds are able to leverage small variations in their pitch to continuously optimize their song performance [30], and humans actively reshape the structure of their motor output variability to elicit faster learning of reaching tasks [31]. We found that natural gait variability did not initiate the optimization process in our particular experiment. Instead, subjects persevered at their initial preferred step frequency after the controller was turned on, even though minor adjustments to step frequency would have resulted in a more economical gait. Only after the exploration period, which enforced large variations in step frequency, did subjects demonstrate large adaptations toward the new energetic optima (Figure 3A). One possible explanation for this need for exploration is that people's natural variability in step frequency is not expansive enough to elucidate a clear energetic gradient. Alternatively, people may not initiate optimization based on energetic gradients, but may instead require that exploration provide explicit experience with the new optimum in order for people to adapt to it. In either case, these may be smaller issues when walking in a real-world setting because natural changes in speed and terrain may generate the

variability in gait required to either initiate optimization or provide experience with new optimal movement patterns.

Our findings suggest that new optima are encoded in an updated prediction of the energetically optimal gait and leveraged to rapidly select preferred step frequency [29, 32]. When subjects were held away from their preferred step frequency using a metronome and then released, they returned to their new preferred step frequency within seconds (Figures 3B and 3C). These adjustments are likely too fast to be governed by blood gas sensors, muscle metaboreceptors, and other known direct sensors of energetic cost, which are known to be relatively slow [33, 34]. Furthermore, optimization itself tends to be slow if its algorithm requires the time consuming steps of averaging and iterative convergence [29]. That the subjects made an updated prediction of the optimal gait is also observable at the end of the experiment, when subjects' preferred step frequency remained shifted toward the control function optima for minutes despite a return to the natural energetic landscape (Figure 3B). This aftereffect differs from the aftereffects seen in force-field reaching or split-belt walking paradigms [35, 36], where the resulting trajectories are mirror images of those observed when initially exposed to the novel environment. When our controller was turned off, rather than displaying this overshoot and rapid correction, we instead found that subjects adjusted to the rapid reduction in exoskeleton torque and persevered at the optimum for the previous adaptation. These aftereffects appeared to last an order of magnitude longer than those typically reported in other walking paradigms [36–39]. This implies that sensorimotor predictions about energetically optimal movements are particularly resilient, at least without an exploratory phase to initiate re-optimization. The slow step-frequency adjustments during re-adaptation are not in conflict with the fast adjustments observed when subjects are released from a metronome after exploring their new energetic landscape. During the latter, subjects are able to quickly predict their optimal gait within a now-familiar energetic landscape. But the former requires optimization within a new energetic landscape, or at least recognition that this new landscape is familiar.

Despite a lifetime of experience walking under natural conditions, people readily adapted established motor programs to minimize energy expenditure, and they did so for quite small energetic gains. It is sensible that motor programs remain malleable because people's bodies, and the tasks they are presented with, can change. Continuous energetic optimization benefits motor adaptation by keeping movements close to energetically optimal, helping people to efficiently adapt to changing terrains, compensate for injury or motor deficits, and learn new tasks.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and one figure and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.08.016>.

AUTHOR CONTRIBUTIONS

J.C.S. and J.M.D. designed the study with input from S.M.O. and J.D.W.; J.C.S. collected data and performed analysis; and J.C.S. and J.M.D. wrote the manuscript. All authors discussed the results and commented on the manuscript.

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REFERENCES

1. Srinivasan, M., and Ruina, A. (2006). Computer optimization of a minimal biped model discovers walking and running. *Nature* **439**, 72–75.
2. Donelan, J.M., Kram, R., and Kuo, A.D. (2001). Mechanical and metabolic determinants of the preferred step width in human walking. *Proc. Biol. Sci.* **268**, 1985–1992.
3. Bertram, J.E., and Ruina, A. (2001). Multiple walking speed-frequency relations are predicted by constrained optimization. *J. Theor. Biol.* **209**, 445–453.
4. Zarrugh, M.Y., Todd, F.N., and Ralston, H.J. (1974). Optimization of energy expenditure during level walking. *Eur. J. Appl. Physiol. Occup. Physiol.* **33**, 293–306.
5. Molen, N.H., Rozendal, R.H., and Boon, W. (1972). Graphic representation of the relationship between oxygen-consumption and characteristics of normal gait of the human male. *Proc. K. Ned. Akad. Wet. C.* **75**, 305–314.
6. Elfman, H. (1966). Biomechanics of muscle with particular application to studies of gait. *J. Bone Joint Surg. Am.* **48**, 363–377.
7. Ralston, H.J. (1958). Energy-speed relation and optimal speed during level walking. *Int. Z. Angew. Physiol.* **17**, 277–283.
8. Atzler, E., and Herbst, R. (1928). *Arbeitsphysiologische Studien III*. *Pflugers Arch.* **215**, 292.
9. Alexander, R.M. (1996). *Optima for Animals* (Princeton University Press).
10. Umberger, B.R., and Martin, P.E. (2007). Mechanical power and efficiency of level walking with different stride rates. *J. Exp. Biol.* **210**, 3255–3265.
11. Minetti, A.E., Capelli, C., Zamparo, P., di Prampero, P.E., and Saibene, F. (1995). Effects of stride frequency on mechanical power and energy expenditure of walking. *Med. Sci. Sports Exerc.* **27**, 1194–1202.
12. Holt, K.G., Hamill, J., and Andres, R.O. (1991). Predicting the minimal energy costs of human walking. *Med. Sci. Sports Exerc.* **23**, 491–498.
13. Rodman, P.S., and McHenry, H.M. (1980). Bioenergetics and the origin of hominid bipedalism. *Am. J. Phys. Anthropol.* **52**, 103–106.
14. Sockol, M.D., Raichlen, D.A., and Pontzer, H. (2007). Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc. Natl. Acad. Sci. USA* **104**, 12265–12269.
15. Alexander, R.M. (2001). Design by numbers. *Nature* **412**, 591.
16. Ivanenko, Y.P., Dominici, N., and Lacquaniti, F. (2007). Development of independent walking in toddlers. *Exerc. Sport Sci. Rev.* **35**, 67–73.
17. Tucker, V.A. (1970). Energetic cost of locomotion in animals. *Comp. Biochem. Physiol.* **34**, 841–846.
18. Alexander, R.M. (1989). Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* **69**, 1199–1227.
19. Shadmehr, R., and Mussa-Ivaldi, S. (2012). *Biological Learning and Control* (MIT Press).
20. Todorov, E., and Jordan, M.I. (2002). Optimal feedback control as a theory of motor coordination. *Nat. Neurosci.* **5**, 1226–1235.
21. Franklin, D.W., and Wolpert, D.M. (2011). Computational mechanisms of sensorimotor control. *Neuron* **72**, 425–442.
22. Emken, J.L., Benitez, R., Sideris, A., Bobrow, J.E., and Reinkensmeyer, D.J. (2007). Motor adaptation as a greedy optimization of error and effort. *J. Neurophysiol.* **97**, 3997–4006.
23. Finley, J.M., Bastian, A.J., and Gottschall, J.S. (2013). Learning to be economical: the energy cost of walking tracks motor adaptation. *J. Physiol.* **591**, 1081–1095.
24. Huang, H.J., Kram, R., and Ahmed, A.A. (2012). Reduction of metabolic cost during motor learning of arm reaching dynamics. *J. Neurosci.* **32**, 2182–2190.
25. Bunderon, N.E., Burkholder, T.J., and Ting, L.H. (2008). Reduction of neuromuscular redundancy for postural force generation using an intrinsic stability criterion. *J. Biomech.* **41**, 1537–1544.
26. Burdet, E., Osu, R., Franklin, D.W., Milner, T.E., and Kawato, M. (2001). The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature* **414**, 446–449.
27. Latt, M.D., Menz, H.B., Fung, V.S., and Lord, S.R. (2008). Walking speed, cadence and step length are selected to optimize the stability of head and pelvis accelerations. *Exp. Brain Res.* **184**, 201–209.
28. Marsh, A.P., Martin, P.E., and Sanderson, D.J. (2000). Is a joint moment-based cost function associated with preferred cycling cadence? *J. Biomech.* **33**, 173–180.
29. Snaterse, M., Ton, R., Kuo, A.D., and Donelan, J.M. (2011). Distinct fast and slow processes contribute to the selection of preferred step frequency during human walking. *J. Appl. Physiol.* **110**, 1682–1690.
30. Turner, E.C., and Brainard, M.S. (2007). Performance variability enables adaptive plasticity of 'crystallized' adult birdsong. *Nature* **450**, 1240–1244.
31. Wu, H.G., Miyamoto, Y.R., Gonzalez Castro, L.N., Ölveczky, B.P., and Smith, M.A. (2014). Temporal structure of motor variability is dynamically regulated and predicts motor learning ability. *Nat. Neurosci.* **17**, 312–321.
32. Davidson, P.R., and Wolpert, D.M. (2005). Widespread access to predictive models in the motor system: a short review. *J. Neural Eng.* **2**, S313–S319.
33. Craig, A.D. (2003). Interoception: the sense of the physiological condition of the body. *Curr. Opin. Neurobiol.* **13**, 500–505.
34. Marshall, J.M. (1994). Peripheral chemoreceptors and cardiovascular regulation. *Physiol. Rev.* **74**, 543–594.
35. Shadmehr, R., and Mussa-Ivaldi, F.A. (1994). Adaptive representation of dynamics during learning of a motor task. *J. Neurosci.* **14**, 3208–3224.
36. Reisman, D.S., Block, H.J., and Bastian, A.J. (2005). Interlimb coordination during locomotion: what can be adapted and stored? *J. Neurophysiol.* **94**, 2403–2415.
37. Blanchette, A., and Bouyer, L.J. (2009). Timing-specific transfer of adapted muscle activity after walking in an elastic force field. *J. Neurophysiol.* **102**, 568–577.
38. Fortin, K., Blanchette, A., McFadyen, B.J., and Bouyer, L.J. (2009). Effects of walking in a force field for varying durations on aftereffects and on next day performance. *Exp. Brain Res.* **199**, 145–155.
39. Choi, J.T., and Bastian, A.J. (2007). Adaptation reveals independent control networks for human walking. *Nat. Neurosci.* **10**, 1055–1062.