

So, the mitochondrion of *B. motovehiculus* seems to be dismantling its electron transport chain Complexes III and IV and its ATPase and turning into a *Blastocystis/Nyctotheris* kind of mitochondrial organelle [8]. The process, however, suggests that Nature is not a blunt butcher but actually a rather skilled surgeon when adapting to new environmental challenges.

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Motor Control: No Constant but Change

J. Maxwell Donelan

Department of Biomedical Physiology & Kinesiology, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada
 Correspondence: mdonelan@sfu.ca
<http://dx.doi.org/10.1016/j.cub.2016.09.001>

We rely on predictions to rapidly select our walking gaits. New research suggests that the formation of these predictions is driven by the difference between the walk we expect and the walk we get.

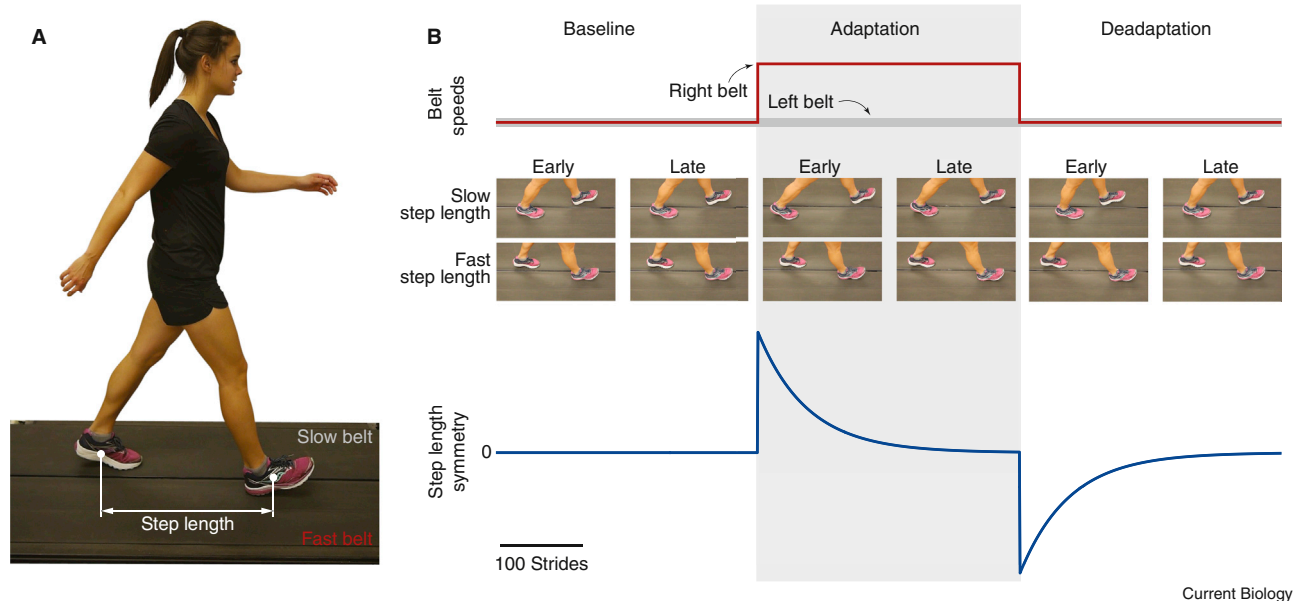
There is a path that I have walked more than any other. It runs from my family cottage down a steep hill to a small lake. The path, which is as often slick as it is dry, traces a rather convoluted pattern to avoid the rocky obstacles where the Canadian Shield pushes through the surrounding soil. The path challenged me as a child with a growing body and still does when my squirming children are riding on my shoulders. How is walking so adept at getting us to where we want to be, even when our bodies and the environment are continuously changing? A new study by Roemmich *et al.* [1],

reported in this issue of *Current Biology*, delivers important new insight into how our nervous system uses prediction to help generate our skillful walking.

Walking is not only about getting to a destination without falling over. People also prefer, for example, to walk in ways that minimize their energetic cost [2,3] and to arrive within a certain time [4,5]. Thus, one task for the nervous system is to coordinate the hundreds of muscles at its disposal to optimize an objective that involves stability, energy and time [6]. Each muscle has a range of forces that it

can deliver, and these forces can be adjusted about every millisecond. As a result, the nervous system can select from a huge number of possible control strategies, involving many muscles, many levels of force, many periods of time. This flexibility in control is certainly a benefit to the nervous system, as it increases the likelihood that there exist good solutions to a particular walking problem. But it also presents a challenge — there are too many strategies for the nervous system to search through the possibilities within the few steps available in a typical walking bout.





Current Biology

Figure 1. The basics of split-belt treadmill walking.

(A) These treadmills have two belts that run side-by-side, and participants walk with one foot on each belt. Step length is defined as the distance between the two feet at the instant the swing leg contacts the ground. A walking stride has two step lengths — one where the right leg is in front (shown) and one where the left leg is in front (not shown). It is convention to distinguish between the two step lengths by naming them after the speed of the belt under the front leg during adaptation. This image illustrates the fast step length. (B) The experimental design has three periods: baseline, adaptation and deadaptation. During baseline, the belts are moving at equal speeds (top panel lines). At the onset of adaptation, speed is increased for the right belt (thin red line) while the left belt speed is kept constant (thick grey line). After a time, the fast belt is returned to the original speed, demarking the onset of deadaptation. Each of these periods is long enough for subjects to take hundreds of strides. During baseline, movements of the left and right legs are symmetrical and the two step lengths are equal (middle panel photos). But at the onset of adaptation, the right leg gets dragged quite far backwards by the fast belt before the swinging left leg contacts the ground — the slow step length immediately becomes longer. It is convention to compare the two step lengths with a single metric called *step length asymmetry* (bottom panel lines). Deviation of this metric from zero, in either direction, indicates increased step length asymmetry. Belt speed changes at the onset of adaptation and deadaptation both result in step length asymmetries. And in both cases, the nervous system adapts its predictions over the next few hundred strides, eventually restoring symmetrical step lengths.

The nervous system mitigates this curse of dimensionality by predicting the best control strategies [7]. For example, if you are walking on a treadmill and the speed is unexpectedly increased, your nervous system will not treat walking at this new speed as an entirely new problem to solve and begin a search through all the candidate control strategies. Instead, it will immediately adjust step frequency, step width and other aspects of your gait towards what it has previously learned is the optimal combination of parameters for the new speed [2,8]. And the nervous system gets most of the way towards the final steady-state strategy in just a few walking steps [8]. These predictions are normally subconscious, but you may become aware of them when you are fooled into using them incorrectly. A broken escalator, for example, is just like a familiar staircase, but walking up it feels strange because we anticipate the dynamics of one that works [9].

Predictions, although rapid, are prone to error when conditions are unfamiliar. Scientists have used this limitation as an opportunity to expose our predictions to analysis. They have used a variety of ingenious methods that include robotic devices to apply unfamiliar forces to the reaching hand [10], and prism goggles to create unfamiliar shifts in visual perception [11]. Amy Bastian, the senior author of the new study [1], and her colleagues have championed the use of split-belt treadmills to uncover fundamentals of prediction in walking [12] and how they are applied to improve gait in clinical populations [13].

Here's how these split-belt treadmill experiments work (Figure 1). The treadmill is like any other except that there are two belts that run side-by-side, and participants walk with one foot on each belt. The basic experimental design begins with a baseline period where the two belts move at the same slow speed.

This is a familiar condition — the special treadmill is behaving like a typical one, and walking on a good treadmill is physically equivalent to walking over ground [14]. Consequently, participants rapidly adopt their preferred gait. During the next period, termed adaptation, the speed of one belt is doubled to a typical walking speed, while the other belt remains at the original slow speed. In response, the right and left legs immediately move asymmetrically — the control strategy that normally produces symmetrical walking now poorly predicts it. The authors track an aspect of this asymmetry by comparing the lengths of the steps taken on the two belts (Figure 1). What happens next is the key characteristic of split-belt walking that makes it useful for studying adaptation. With each new stride in this novel condition, the nervous system adjusts its control strategy bringing the two step lengths closer to symmetry. After a few hundred strides, step length

symmetry is nearly perfectly restored. The time course of these gait adjustments are used to characterize how quickly the nervous system adapts its prediction.

The final period of this basic experimental design, termed deadadaptation, provides strong evidence that the nervous system has indeed adapted. The researchers return the fast belt speed to the original slow belt speed, and the belt speeds are again equal. These conditions are more than familiar, yet participants do not immediately walk normally. Instead, they apply the new prediction that they just learned on the split belts, causing them to use an asymmetrical gait that is, in many ways, opposite to that which they selected at the beginning of adaptation. This aftereffect is salient and persistent — participants now feel the illusion that their legs are moving at different speeds [15], and they will limp their way out of the lab if not given enough time to unlearn their new control strategy [16]. As with the adaptation period, step lengths gradually get more symmetric over the next few hundred strides.

In the new study, Roemmich *et al.* [1] used this basic experimental design to test an idea about how the nervous system adapts its predictions to new conditions. They theorized that the nervous system not only has a prediction about what motor commands will produce the desired gait, but that it also has a prediction about the sensory feedback that will result from that motor command. The nervous system then compares the predicted feedback against the actual sensory feedback received after executing the motor command. When the belt speeds are first split, for example, the nervous system executes its preferred motor commands and expects a symmetric gait but receives feedback that the gait was highly asymmetric. The authors theorize, as others have before them [7,17], that the nervous system uses this sensory prediction error between expected and actual sensory signals to adapt the motor command to one that returns the gait to symmetry.

There is a surprising implication of this theory: coaching people to use the

correct motor commands does not accelerate how quickly they learn to walk symmetrically on their own. This is because the nervous system must still learn the new relationship that maps motor commands to sensory feedback even when performing the task perfectly. Roemmich *et al.* [1] leveraged this implication to provide a strong test of their theory. They coached participants to produce symmetrical step lengths during adaptation by showing participants their level of gait asymmetry and instructing them to reduce it. This was accomplished using a task that was a bit like a video game, as well as more conventional real-time videos of their walking legs. It worked — the coached participants converged more quickly on symmetrical step lengths than those that did not receive the visual feedback. But when the researchers allowed the participants to fully acquire the step length symmetrical gait and then removed the visual feedback, participants immediately reverted to an asymmetrical gait even though they just walked with symmetrical step lengths for dozens of steps. Next, the researchers removed the visual feedback at different periods of the adaptation and deadadaptation stages and found that the underlying rate of adaptation was unaffected by prior practice of walking symmetrically. These results are perhaps counterintuitive, especially if you are a coach of some sort, yet entirely consistent with the ideas of Roemmich *et al.* [1] about sensory prediction error driving adaptation. They are also remarkably consistent with earlier work [17] that studied arm reaching rather than walking, and perturbed the task using visual rotations rather than changes to belt speed, suggesting that the present findings apply to movement control in general.

The nervous system's desire for step length symmetry is a curious finding. Symmetric gaits have some intrinsic appeal, but complete symmetry is impossible when treadmill belts are moving at different speeds. For example, the increases in step length symmetry that occur during adaptation require the nervous system to decrease symmetry in stance duration [18]. Why does the nervous system prioritize step

length symmetry over others? One explanation is that this aspect of symmetry is not a high-level control goal but instead arises as the nervous system optimizes for walking's energy, stability, and time. In support of this view, Bastian and her colleagues [19] have previously found that minimizing energetic cost is a key criterion driving adaptation during the same split-belt walking paradigm. And recent research from my own group [20] has demonstrated that people will adapt their gait to converge on new energetic minima, even for remarkably small cost savings.

These split-belt treadmill experiments, and others like them, may give the wrong impression that our nervous systems only need to adapt when experiencing large and infrequent perturbations. But as we walk through our lives, we are constantly experiencing change both within the world around us and within our own bodies. Refining our walking skill requires our nervous systems to also continue to change. While adaptation may be key to achieving our skillful movements, our biomechanical and neural capabilities do place bounds on what it can achieve. My cottage path will soon reflect these limitations — my father is turning 75 this year, and we are replacing the path with comfortable and consistent wooden steps.

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Zoology: At Last an Exit for Ctenophores

Gonzalo Giribet

Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, 26 Oxford Street, Cambridge, MA 02138, USA

Correspondence: ggiribet@g.harvard.edu

<http://dx.doi.org/10.1016/j.cub.2016.08.036>

Ctenophores, one of the most basal branches in the tree of life, have been found to have a through-gut, complete with mouth and anus. Basal animals are surprisingly complex and simplification has been rampant in animal evolution.

It has been generally accepted that life in general and animals in particular evolved from simple forms to more complex ones. Early evolving animals lacked tissues or a basement membrane isolating their internal milieu from the environment. Then with tissue-level integration, guts and nervous systems evolved, and the gut, which started as a simple blind sac-like structure, became more complex, regionalized, and acquired a second opening, with a mouth and an anus. But does this evolutionary sequence reflect what really happened? In an elegant new article in this issue of *Current Biology*, Presnell and collaborators [1] demonstrate that comb jellies (members of the animal phylum Ctenophora) possess a through-gut, with a mouth for ingesting their prey and two fully-functioning anal pores — the latter is the

key discovery. These anal pores were already reported in the nineteenth Century by Louis Agassiz [2] but had been thought to be mostly non-functional. Now, Presnell and collaborators [1] were able to demonstrate the active use of the anal pores in two ctenophore species, *Mnemiopsis leidyi* and *Pleurobrachia bachei*, kept in captivity in laboratories on the east and west coasts of the U.S. (Figure 1). This behavior was also observed in free-living specimens of a multitude of ctenophore genera.

Comb jellies are mostly macro-pelagic (from a few centimeters to almost 1.5 meters in body length) and exclusively marine animals of a gelatinous consistency, nearly all of which spend their lives in the water column. A handful of benthic species, including a sessile one, are known. There are between

150 and 250 described species, but due to their gelatinous nature, they are difficult to collect and study, and thus many remain to be formally described. Ctenophores have been reported to live at the water's surface, where they can be locally abundant, to depths exceeding 7000 meters.

Ctenophores are the largest animals to swim by ciliary action. For this, they use their characteristic rows of iridescent ciliary plates (hence their name combs or ctenes) that are present at least during some part of their life cycle. In addition to ciliary action, ctenophores can also move by muscular contraction of their lobes, or use their musculature to withdraw the retractable tentacles into tentacular sheaths. They are carnivorous, feeding on other small pelagic and planktonic animals, often captured by a pair of tentacles loaded with a special