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Motor Learning: The Great Rate Debate

Recent research shows that our innate capacity to adapt our movements to compensate for changes to our body or the environment is far more susceptible to modulation by experience than previously thought.

Adrian M. Haith¹
and John W. Krakauer^{1,2}

A constantly changing world and body mean that the same motor commands will not always lead to the same outcome. Consequently, our motor commands require continuous adjustment to maintain accurate performance [1,2]. Artificial changes in the environment can be created in the laboratory either by distorting visual feedback or by applying a force field to the arm: subjects readily adapt to these perturbations to restore baseline performance, usually within around 10–30 movements following an exponential timecourse. It has long been known that this process can be accelerated by prior experience [3–5]. Examining precisely when such changes in learning rate do or do not occur offers a critical window into the underlying organization of the motor system [3,6,7]. A study [8] published in this issue of *Current Biology* shows that, with the right kind of manipulation, much more dramatic changes in learning rate can be achieved than previously thought possible.

The question of why learning rates change leads immediately to the

question of why learning has a rate at all. Why should subjects not be able to adapt to a perturbation in a single shot? Why should it take around 20 trials to adapt and not just three to four trials, or hundreds of trials? Another way to put this question is: how much should one be willing to learn from a single movement? A popular answer to this question appeals to a Bayesian view of the motor system [2,9,10]. According to this view, subjects possess a probabilistic model of the environment: how it will affect movements now, and how it is liable to change in the future. Each movement is selected according to the subject's best prediction about the current state of the environment. If, after the movement is made, the prediction turns out to be wrong, the estimated state of the environment is revised by weighing up uncertainty in the predicted state of the environment against uncertainty in the new observation (that is, whether the error was actually caused by the environment). This revised estimate is then used as the basis for predicting the state of the environment in the next trial, and so forth. Thus, the key power of this theory is that it can potentially explain learning rates as being derived

from underlying noise and variability. Subjects should proceed with caution and adapt slowly if observations are unreliable and/or if experience tells them that the environment does not usually change much. But, if they have high confidence in their sensory feedback and/or expect a volatile environment, they should adapt quickly.

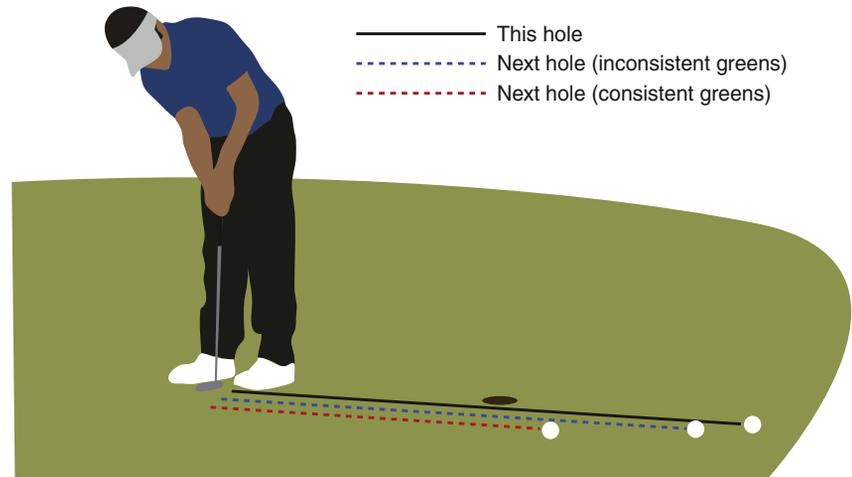
This Bayesian theory of motor adaptation has been partially supported by experiment. Increasing uncertainty in visual feedback, for example by blurring it, slows down adaptation [10,11]. However, attempts to increase learning rate by making the environment more variable have been less successful [10,12]. In their new work, Gonzalez Castro *et al.* [8] changed the variability of the environment by making the force field follow a random walk from trial to trial. They found that training subjects with this fluctuating force field had little effect on learning rates compared to naïve subjects.

The key contribution of this paper, however, is to show that learning rates *can* be changed significantly by prior experience if the right manipulation is used. The critical trick is not to use a random walk to generate variability in the environment, as previous approaches have tried, but instead to change the environment in a step-wise fashion, switching between different, fixed force fields. The authors demonstrate that it is not the variability of the environment that modulates learning but the *consistency* of the environment — how likely it is that the current environmental state will persist

for another trial. If subjects are taught that once a perturbation comes on abruptly, it tends to stick around, then they learn more from a single movement (see example in Figure 1). Conversely, if subjects are taught that perturbations are usually transient, they learn less from a single movement. Importantly, however, they do continue to adapt a little, even when experience tells them that perturbations only ever last for one trial then disappear.

It is tempting to conclude from these findings that consistency is the 'right' knob to turn to crank the motor system's learning rate up or down. However, further results from the paper question whether we should consider 'rate' to be the defining property of the way the motor system learns. Gonzalez Castro *et al.* [8] show, strikingly, that the adaptive response can not only be down-regulated but can even be reversed. Most groups of subjects were trained in an environment in which there was either no force, or a rightward force. If subjects suddenly experienced a previously-unseen leftward force, they responded on the next trial more like it had been a rightward force. Quantifying a learning rate from these trials leads to the absurd scenario of a *negative* learning rate. This surprising result illustrates clearly that changes in observed learning rate should not necessarily be interpreted as modulating the sensitivity to error. Instead, a fundamentally different mechanism may be in operation.

Although the findings in this paper are inconsistent with existing incarnations of Bayesian motor learning, they do not wholly refute the hypothesis that motor learning obeys Bayesian principles. Within existing theories, prior experience can only alter behavior by changing subjects' prior beliefs about incremental changes in the environment from trial to trial as it follows a random walk. This random-walk premise leads directly to the notion that learning rate is the key characteristic of the motor system. However, one can envisage more general Bayesian models in which subjects build prior beliefs about the actual states of the environment (rather than over incremental trial-to-trial changes) and about the switching dynamics of the environment; that is, they can build more accurate models of the statistics of the environment than simple random walks.



Current Biology

Figure 1. Motor adaptation and environmental consistency.

After over-hitting a putt, how should you adjust your swing for the next shot? Although the miss may have been due to one-off execution noise, it might have been due to properties of the green being different from the previous hole. The findings by Gonzalez Castro *et al.* [8] suggest that you will compensate for this error more quickly if conditions are reliably consistent from green to green.

Such models would predict richer behavior than simple learning rate modulation and may have more success in accounting for the results of Gonzalez Castro *et al.* [8]. Given that there is growing evidence of explicit, cognitive involvement in motor adaptation paradigms [13–15], it may not be so surprising that the motor system can exhibit a high degree of flexibility and sophistication in inferring the exact structure of variability in the environment. The more profound puzzle, perhaps, is why the motor system is unable to do any better and still fails to adapt in a single shot in highly consistent environments and still continues to adapt a little in inconsistent ones.

It remains unclear how these results, obtained through extensive training in particular sequences of force fields, relate to the more elementary phenomenon of savings — when learning rates are faster the second time a perturbation is experienced. Increases in learning rate associated with savings are generally much lower than the increases Gonzalez Castro *et al.* [8] were able to demonstrate. Does savings occur because the motor system has slightly revised its beliefs about the consistency of the environment? Or, conversely, do the effects seen here reflect an amplification of the mechanisms that drive savings?

Recent theories suggest that the rate change that characterizes savings is caused by a recall of previously successful actions that have been repeated in the past [7,16], not a change in sensitivity to error. This idea is certainly consistent with the reversal of learning rates described above. Manipulating environmental consistency may simply be an extremely effective way to enhance this process of learning and retrieving an appropriate set of actions. It is not clear, however, how decreases in learning rate could be explained by such a mechanism. It is possible that increases and decreases in observed learning rate occur by different means, with increases brought about through a retrieval mechanism and decreases reflecting a genuine decrease in sensitivity to error. Further work will be required to clearly demarcate the relative contributions of error-driven processes and recall to changes in observed learning rate.

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Evolution: Predator versus Parasite

Both predators and brood parasites can be major threats to the reproduction of many birds. A new study shows that some cuckoo chicks can help deter nest predators, potentially improving host reproductive success when predation risks are high.

Martin Stevens

As Tennyson once famously wrote, nature is “red in tooth and claw”, and antagonistic interactions among species are ubiquitous in the natural world. These often result in evolutionary arms races, with each party fighting to stay ahead of the other. Two of the most common interactions are predator–prey and brood parasite–host relationships [1]. Many breeding birds face both of these threats: nest predation is extremely common, but some birds face the added risk of also being duped into rearing completely unrelated offspring. Here, brood parasites such as various cuckoo species, lay their eggs in the nests of other birds, so that the hosts or foster parents rear the chick instead and incur the costs of parental care. While many hosts of cuckoos and other parasites show defences against the intruders (such as mobbing adult cuckoos or rejecting foreign eggs [2–4]), not all do. A new study by Canestrari *et al.* [5] shows that there may sometimes actually be a benefit to having a brood parasite in the nest, by virtue of protection from predators, and that this may explain a lack of host defences.

In northern Spain, carrion crows (*Corvus corone corone*) are parasitized

by the great spotted cuckoo (*Clamator glandarius*). Unlike some other brood parasites, the great spotted cuckoo chick does not evict or kill the host’s offspring, but is instead reared alongside them, meaning that host young can survive and fledge in many nests (Figure 1). Offspring of the great spotted cuckoo secrete a foul smelling repellent substance that has been suggested to deter predators (Figure 2), and Canestrari *et al.* [5] theorised that the presence of a cuckoo chick in the host nests might also aid the other host chicks present. The authors combined three lines of exploration to test this idea. First, they used data from 16 years of crow reproductive success in the field. Next, they conducted experiments whereby they manipulated some crow nests by adding one or two cuckoo chicks, removing cuckoos, or leaving some nests unmanipulated (both with and without a parasite). Finally, the authors analysed the composition of the chemicals the cuckoo chicks secreted, and undertook tests on three potential nest predator groups (cats, crows, and raptors) to determine its effect on deterring them from food (meat pieces either treated with the cuckoo secretion or simply with water).

The long-term data showed that parasitized nests were more likely

than unparasitized nests to produce at least one crow chick to fledging (a 76% versus 54% chance of success). However, among nests that produced at least one young, fewer host offspring were fledged in nests with cuckoos than those without. The net effect effectively meant that there was no clear difference in the overall number of crows fledged in nests that were parasitized with those that were not. The nest manipulations supported this data. When cuckoo chicks were removed, nest success declined from about 60% to just 31%. In contrast, adding a cuckoo chick increased success from around 38% to 71%. Reassuringly, the magnitude of the changes was very similar in each data set, and in contrast, simply moving crow chicks between nests had no effect on success. In the behavioural assays of how predators avoid cuckoo chicks, all three potential predator groups were less likely to eat the meat treated with the secretions than the control pieces. Chemical analyses also showed that the secretions comprised several repulsive compounds, including acids, phenols, and sulphur-containing compounds, many of which were not present or present at lower amounts in the crow faeces.

These combined pieces of evidence led the authors to conclude that the most likely explanation for the nest success results is that cuckoo chicks reduce the risk of predation through the chemical secretions that they produce. The authors argue that depending on the intensity of predation each year, the relationship between cuckoo and host effectively switches from parasitism to