

# Understanding sensorimotor adaptation and learning for rehabilitation

Amy J. Bastian

Kennedy Krieger Institute, Department of Neuroscience, Neurology, and Physical Medicine and Rehabilitation, The Johns Hopkins School of Medicine, Baltimore, Maryland, USA

Correspondence to Dr Amy J. Bastian, PhD, PT, Kennedy Krieger Institute and Departments of Neuroscience, Neurology, and Physical Medicine and Rehabilitation, The Johns Hopkins School of Medicine, Baltimore, MD 21205, USA

**Current Opinion in Neurology** 2008, 21:628–633

## Purpose of review

Understanding the behavioral mechanisms of sensorimotor adaptation and learning is essential for designing rational rehabilitation interventions.

## Recent findings

Adaptation is the trial-and-error process of adjusting movement to new demands and is now thought to be more than a simple error cancellation process. Instead, it may calibrate the brain's prediction of how the body will move and takes into account costs associated with the new task demand. Damage of the cerebellum systematically disrupts adaptation, but damage to other brain regions often does not. Adapting to perturbations driven by a device like a robot or a treadmill leads to only partial generalization to unconstrained 'real-world' movements. Repeated adaptation can lead to learning a new motor calibration, but process of consolidation of this type of learning is less understood in patients.

## Summary

Adaptation is inherently important for rehabilitation by making movement flexible, but can also be used to ascertain whether some patients can generate a more normal motor pattern. Repeated adaptation can lead to learning of a new, more permanent motor calibration. Though less understood, this type of learning is likely to be an important method for making long-term improvements in patients' movement patterns.

## Keywords

memory, motor, reaching, stroke, walking

Curr Opin Neurol 21:628–633  
© 2008 Wolters Kluwer Health | Lippincott Williams & Wilkins  
1350-7540

---

## Introduction

Human movement control is complex – over 600 muscles act together to control the movement of a couple of hundred bones. Yet, we make smooth and accurate movements with ease, even in the face of constantly changing demands. We often take for granted the processes that allow this flexibility, only becoming aware of the challenges that face the central nervous system (CNS) when something goes wrong. This review will focus on two phenomena thought to be critical for motor flexibility, namely motor adaptation and motor learning. I will define these terms, compare and contrast known behavioral processes, discuss effects of brain lesions, and address the ramifications for rehabilitation.

---

## Adaptation

Consider the following situation: you borrow a friend's computer, but find that the mouse moves the cursor faster than you expect, resulting in inaccuracies (and annoyance). Luckily, it only takes a matter of minutes for your brain to adjust and account for the new mouse–cursor

settings. However, when you return to your own computer, you temporarily make errors as a result of your experience on your friend's computer. This phenomenon is indicative of an error-driven motor calibration process called motor adaptation.

## Definition

The term motor 'adaptation' has previously been used by different groups to refer to distinct human motor behaviors [1,2]. Here, I will use the definition of adaptation from Martin *et al.* [2]. It is the modification of a movement from trial-to-trial based on error feedback in which the following criteria are met. First, the movement retains its identity of being a specific action (e.g. 'reaching') but changes in terms of one or more parameters (e.g. the pattern of force or direction). Second, the change occurs with repetition or practice of the behavior and is gradual over minutes to hours. Third, once adapted, individuals cannot retrieve the prior behavior; instead, they show 'after-effects' and must 'de-adapt' the behavior with practice in the same gradual, continuous manner back to the original state.

Why is adaptation important for human behavior and rehabilitation, given its relatively transient nature? The answer is simple: it allows the nervous system a highly flexible control that can account for temporary, but predictable, changes in the demands of the task. Thus, a finite number of ‘learned’ motor patterns can be adapted to account for many different situations.

### Behavioral findings

Adaptation occurs for all types of movements such as reaching, walking, balancing, and eye movements [3–6]. Adaptation typically occurs with practice over tens to hundreds of movements, approximately on a timescale of minutes to hours. The rate of de-adaptation is often faster than the rate of adaptation [7,8]. It is thought that the number of times that a movement is practiced is the more relevant training signal than the amount of time that has passed, though there is probability of some interaction between the two [9<sup>•</sup>]. Indeed, short delays (i.e. 4s) between movements can augment the adaptation process, possibly through a persisting memory trace of the error [9<sup>•</sup>]. There is also good evidence that adaptation may consist of two processes – one is faster but transiently stored and one that is slower and more persistently stored [8]. Understanding whether the fast and slow processes rely on distinct neural mechanisms and how to differentially engage them would benefit rehabilitation training. Finally, several studies suggest that this process is somewhat automatic – in other words, patients do not have to attempt to ‘consciously’ make corrections in their movement. The adaptation proceeds regardless of this [2,10].

What drives adaptation? When a given movement, such as a reach, is perturbed, the nervous system attempts to reduce the error from one reach to the next. Recent work suggests that an important signal is a sensory prediction error, which is the difference between the brain’s predicted outcome of the movement and the observed outcome [11<sup>•</sup>]. Note that this is different than an error in target accuracy – it instead reflects whether the body moved in the way that the brain thought it would [12<sup>•</sup>]. Sensory prediction errors can be used to calibrate the internal representations of body dynamics and the environment and recalibrate for changes in either. Well calibrated internal representations are important because they allow us to decrease reliance on time-delayed feedback from body sensors.

During adaptation, the brain may also alter the movement pattern to minimize the ‘costs’ associated with a consistent perturbation [13,14,15<sup>•</sup>,16<sup>•</sup>]. Costs might include energy demands, forces, fatigue, inaccuracy, jerkiness, among others. For any situation, the nervous system has to decide which costs are most important to reduce to achieve the goal of the task. Recent studies suggest that this process is important during walking and

reaching adaptation to force fields. Emken *et al.* [15<sup>•</sup>] studied force perturbations at the foot during walking and found that a model minimizing the kinematic error and effort costs explained adaptation during this task. This is in contrast to most studies that have modeled the process purely as kinematic error cancellation. In a study of reaching in novel force fields, Izawa *et al.* [16<sup>•</sup>] provided compelling evidence that adaptation involves recalibration of internal representations of body dynamics using sensory prediction errors and reoptimization of the motor plan to minimize the costs of the task.

In sum, adaptation represents a more complex process than simply canceling out perturbations. It involves calibrating the brain’s prediction of how the body will move, and probably takes into account costs associated with the task.

### Effects of lesions

Motor adaptation has been studied extensively across patient groups and different types of movement. Damage to the cerebellum most consistently impairs this process by decreasing trial-by-trial improvements during adaptation to a new demand and diminishing the stored after-effect once the demand is removed. This has been shown across many types of movements, including eye movements, arm movements, walking, and balancing [5,17–19]. The type of error information that drives adaptation is not entirely clear, though recent work has shown that sensory prediction errors are sufficient to drive adaptation (i.e. the difference between observed and predicted movement) and that motor corrections that are made after errors do not alter the adaptive process *per se* [11<sup>•</sup>]. In other words, seeing the error on a reach is enough to affect the next reach; correcting the error does not improve this process.

Damage to other parts of the brain has not systematically impaired motor adaptation. Basal ganglia damage from degenerative diseases like Huntington’s or Parkinson’s disease largely leaves the adaptation intact [20–22]. Yet, recent work has suggested that the basal ganglia may be important for assigning cost versus reward values to movement, and therefore might play some role in choosing motor strategy during adaptation [23<sup>•</sup>].

Cerebral damage can slow the adaptation of reaching movements but does not abolish this process [24,25<sup>•</sup>]. Interestingly, cerebral damage does not impair adaptation of walking on a split-belt treadmill and may even produce after-effects that can improve the symmetry of stepping [26<sup>••</sup>].

### Rehabilitation

Devices, such as robots or treadmills, are often used to drive adaptation. An important question for rehabilitation is whether this adaptation generalizes to unconstrained

movements. In other words, does adaptation recalibrate the brain's representation of the person's body or of the novel device? This has been studied in a reaching adaptation task in which people held a robotic arm that perturbed their movement [27,28\*\*]. We found that only 40% of adaptation driven by the robot transferred to reach in free space. This could be improved to 60% if we gradually and implicitly introduce the perturbation, rather than introduce it abruptly at full strength [28\*\*]. These results suggest that gradually changing training conditions that result in smaller trial-to-trial movement errors are more likely to lead to changes in neural representations of the body's dynamics, with broader generalization of the adaptation across conditions.

Is adaptation useful as a rehabilitation treatment? There is a compelling set of studies that have shown that after-effects following a visuomotor adaptation paradigm can positively impact stroke patients with hemineglect [29]. People with hemineglect were studied after adapting a pointing movement while wearing prism goggles that shift gaze to the right. The after-effect from this adaptation caused patients to point toward their left (neglected) side and also improved manual body-midline demonstration and many classical neuropsychological tests. The pointing after-effect is normally short lived in controls, but was shown to be long lasting in people with neglect – the effect lasted 5 days after only one prism exposure where they pointed 50 times [30]. Thus, the longevity of adaptation effects can differ in people with CNS damage, and it is possible to see significant rehabilitative effects from after-effects following adaptation [31].

Even when the after-effects from a single adaptation do not yield long-lasting effects, this process is still extremely important for rehabilitation. Adaptation allows us to determine whether the nervous system is still capable of a more normal pattern of movement. For example, we have recently shown that we can induce after-effects that normalize locomotor symmetry in stroke survivors [26\*\*]. Patients were adapted on a split-belt treadmill where one leg was made to walk twice as fast as the other. After adaptation, they walked with legs at the same speed and showed after-effects that normalized step symmetry and double support times compared to a baseline (i.e. same speed) condition. This means that the CNS retains the capacity to drive the walking pattern more optimally. Similar results have been shown during a reaching adaptation task in stroke survivors [24]. This study found that adapting reaching movements to a force field induced by a robot could cause after-effects that normalized the initial reaching direction.

Important to these studies is how the patients were perturbed during adaptation. Both studies found that adapting the patient to a perturbation that worsened or

amplified their error (rather than correcting it) was what drove adaptation to result in after-effects that improved their movement. In other words, by enhancing their error, the CNS was forced to adapt to correct it. As would be expected, these studies show after-effects that are transient and wash out in 10 min. However, it stands to reason that the CNS would require more training in order to learn to make permanent changes in the pattern. This is discussed in the following section.

---

## Motor learning

At some point in our lives, many of us will have to wear bifocals. Initially, eye movements must be adapted when switching from one magnification to another. This means that the oculomotor system must take some time to re-calibrate every time we switch between lenses. However, with repeated exposure (i.e. adaptation and de-adaptation), the brain can learn two calibrations that it can switch immediately to and from. In other words, no adaptation is required; the desired calibration is learned and accessible.

### Definition

Motor 'learning' is used to mean the formation of a new motor pattern that occurs via long-term practice (i.e. days, weeks, years). After the new movement pattern is learnt, it is stored and can be immediately brought up and used in the appropriate context (i.e. in contrast to adaptation, no practice period is required). Individuals may store many learned motor plans or calibrations that allow for efficient switching from one to another.

There are likely distinct neural and behavioral mechanisms for learning a new movement, depending on the type of motor skill. One form of motor learning is behaviorally tied to the motor adaptation process and will be the focus of this section [2]. Specifically, if individuals adapt and de-adapt repeatedly over weeks of time, they can develop a new 'learned' calibration for the context that initially drove adaptation [2]. In other words, they no longer have to adapt from one behavior to the other, but instead have two learned behaviors that they can switch between. This method of learning may be most ideal for situations in which a person has a previously learned movement that approximates the new movement to be learned. For rehabilitation, this may be an important process. Clinicians are often working with people who can, for example, walk or reach, but their movements are slow, misdirected, inaccurate, or inefficient. One might argue that they do not need to learn the movement from scratch but do need substantial recalibration for their altered neural control.

A second form might be referred to as de-novo motor learning. In this form, many different component motions

are combined, simultaneously or in series, to generate a completely new movement. Take for example, the process of learning to ride a bicycle – pedaling the feet must be combined with balancing on the bike and steering. This is a new skill, as most individuals have nothing like it in their motor repertoire. It must be learnt from scratch. This review will not focus on this type of motor skill learning, as there are other recent and comprehensive reviews [32].

### Behavioral findings

Learning via repeated adaptation has been studied less than single-session adaptation. This type of learning can occur over a period of days to weeks, depending on the task and study. For example, one study repeatedly adapted and de-adapted study participants to prism glasses during a throwing task [2]. Each week, they showed improvement: they were less perturbed when first donning the prisms and showed less of an after-effect when they were removed. By the end of training, they had learnt the appropriate eye–hand coordination pattern for the prisms: they could throw on target immediately when donning or removing the prisms. This demonstrates that repeated adaptations can indeed result in a new, stored calibration that can be used immediately.

Other studies have explored learning of movements over a shorter timescale. For example, participants have been studied adapting reaching to a force or visuomotor perturbation on one day and then returning again minutes, a day, or a week later to retest adaptation. After only one training session, there can be clear evidence of learning indicated by partial retention of the adapted pattern or ‘savings’ (i.e. faster adaptation) on the second test [33]. Studies have also tested for consolidation of the motor pattern, which simply means that it has become resistant to interference caused by adapting to a second opposing perturbation. The results of those studies are mixed: some studies show that the learned pattern is fragile and susceptible to interference until nearly 5 h has passed [34], whereas other studies show it to be fragile no matter what amount of time has passed [35–37]. These discrepancies have not been completely worked out, but one factor that seems to be necessary to see consolidation is a period of practice without the perturbation (i.e. washout) between the perturbed reaches [38]. Also, one must consider whether the interference came before or after the desired motor pattern (i.e. anterograde or retrograde interference). A full review of the consolidation literature, including a synopsis of different types of interference, is detailed in a review of motor consolidation [39].

### Effect of temporary brain inactivation

To date, we know of no studies of individuals with focal brain damage who are undergoing repeated adaptation to learn a movement calibration. However, there are a few

studies using repetitive transcranial magnetic stimulation (rTMS) to cause ‘temporary lesions’ in motor cortical areas. Although not all studies agree, rTMS over primary motor cortex can disrupt consolidation of a learned motor pattern and thus appears to play a role in retaining learning from one day to the next [40–43]. Temporary inactivation of other brain regions has not been studied in the context of learning in this manner.

### Rehabilitation

Motor learning, as defined here, has not been systematically studied for rehabilitative effects. However, we are currently testing whether stroke survivors can learn a new walking calibration through repeated adaptations to a split-belt treadmill over several weeks. The premise is that these individuals will be able to learn a more symmetric stepping calibration through repeated adaptations. However, several open questions exist. If these individuals can learn a new calibration, will it be accessible to them when they are not on the split-belt treadmill? Will they be able to utilize this pattern as their ‘default’ walking pattern? How permanent a change will this be – will it persist days, weeks, or months after the training period? Will continued training be needed to reinforce any change?

### Conclusion

Motor adaptation and learning are two processes fundamental to flexibility of human motor control. Motor adaptation calibrates movement for novel demands. It is not simply an error cancellation process, but instead involves recalibrating the brain’s prediction of how the body will move while also considering the costs of the new demands. Damage of the cerebellum systematically disrupts adaptation, but damage to other brain regions most often does not. Adaptation is inherently important for rehabilitation by making movement flexible, but it can also be used to ascertain whether some patients can generate a more normal motor pattern. Repeated adaptation can lead to learning a new motor calibration. This process is less understood, but might reflect an important method to alter certain patients’ movement patterns on a more permanent basis.

### Acknowledgement

This work was supported by NIH R01 HD048740 and R01 HD40289.

### References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- of outstanding interest

Additional references related to this topic can also be found in the Current World Literature section in this issue (pp. 762–763).

- 1 Deuschl G, Toro C, Zeffiro T, *et al.* Adaptation motor learning of arm movements in patients with cerebellar disease. *J Neurol Neurosurg Psychiatry* 1996; 60:515–519.

- 2 Martin TA, Keating JG, Goodkin HP, *et al.* Throwing while looking through prisms. II: Specificity and storage of multiple gaze-throw calibrations. *Brain* 1996; 119:1199–1211.
- 3 Shadmehr R, Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 1994; 14:3208–3224.
- 4 Reisman DS, Block HJ, Bastian AJ. Interlimb coordination during locomotion: what can be adapted and stored? *J Neurophysiol* 2005; 94:2403–2415.
- 5 Horak FB, Diener HC. Cerebellar control of postural scaling and central set in stance. *J Neurophysiol* 1994; 72:479–493.
- 6 Wallman J, Fuchs AF. Saccadic gain modification: visual error drives motor adaptation. *J Neurophysiol* 1998; 80:2405–2416.
- 7 Davidson PR, Wolpert DM. Scaling down motor memories: de-adaptation after motor learning. *Neurosci Lett* 2004; 370:102–107.
- 8 Smith MA, Ghazizadeh A, Shadmehr R. Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol* 2006; 4:e179.
- 9 Huang VS, Shadmehr R. Evolution of motor memory during the seconds after observation of motor error. *J Neurophysiol* 2007; 97:3976–3985.
- This study shows that adaptation depends not only on the error that a patient makes, but the passage of time between training movements. They also show that the likely mechanisms are that the error trace persists for a short time after the movement is complete, and the nervous system can continue to access it to improve the next movement.
- 10 Mazzoni P, Krakauer JW. An implicit plan overrides an explicit strategy during visuomotor adaptation. *J Neurosci* 2006; 26:3642–3645.
- 11 Tseng YW, Diedrichsen J, Krakauer JW, *et al.* Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J Neurophysiol* 2007; 98:54–62.
- This article asked whether cerebellum-dependent adaptation of reaching relies on sensory or on-line motor corrections. The main finding was that motor corrections during movements did not change adaptation rate, extent or after-effects in healthy controls or individuals with cerebellar damage. Therefore, adaptation to visuomotor perturbations depends on the cerebellum and is driven by the mismatch between predicted and actual sensory outcome of motor commands.
- 12 Miall RC, Christensen LO, Cain O, *et al.* Disruption of state estimation in the human lateral cerebellum. *PLoS Biol* 2007; 5:e316.
- This study tests whether the cerebellum is an important component in predicting the current state of the motor system. Reaching movements were studied and transcranial magnetic stimulation was used to disrupt cerebellar function at focused times. The results suggest that the cerebellum is important for predicting the state of the body during movement in order to avoid long sensory time delays.
- 13 Harris CM, Wolpert DM. Signal-dependent noise determines motor planning. *Nature* 1998; 394:780–784.
- 14 Todorov E. Optimality principles in sensorimotor control. *Nat Neurosci* 2004; 7:907–915.
- 15 Emken JL, Benitez R, Sideris A, *et al.* Motor adaptation as a greedy optimization of error and effort. *J Neurophysiol* 2007; 97:3997–4006.
- This article describes adaptation of leg motions to a systematic perturbation during walking. They show that the adaptation is not merely an error cancellation process, but instead is well predicted by optimizing the cost of error and motor effort during the task.
- 16 Izawa J, Rane T, Donchin O, *et al.* Motor adaptation as a process of reoptimization. *J Neurosci* 2008; 28:2883–2891.
- This study used computational models and human behavioral experiments to test whether reaching adaptation is simply an error cancellation process, or if it takes into account the costs of the movement. Their results suggest that adaptation involves calibrating internal models that predict the sensory consequences of movement and optimization of costs associated with reaching in the environment.
- 17 Lewis RF, Zee DS. Ocular motor disorders associated with cerebellar lesions: pathophysiology and topical localization. *Rev Neurol* 1993; 149:665–677.
- 18 Maschke M, Gomez CM, Ebner TJ, *et al.* Hereditary cerebellar ataxia progressively impairs force adaptation during goal-directed arm movements. *J Neurophysiol* 2004; 91:230–238.
- 19 Morton SM, Bastian AJ. Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking. *J Neurosci* 2006; 26:9107–9116.
- 20 Smith MA, Shadmehr R. Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. *J Neurophysiol* 2005; 93:2809–2821.
- 21 Weiner MJ, Hallett M, Funkenstein HH. Adaptation to lateral displacement of vision in patients with lesions of the central nervous system. *Neurology* 1983; 33:766–772.
- 22 Contreras-Vidal JL, Buch ER. Effects of Parkinson's disease on visuomotor adaptation. *Exp Brain Res* 2003; 150:25–32.
- 23 Mazzoni P, Hristova A, Krakauer JW. Why don't we move faster? Parkinson's disease, movement vigor, and implicit motivation. *J Neurosci* 2007; 27:7105–7116.
- This study of individuals with Parkinson's disease shows that patients can move as fast as controls in a reaching task, but appear to 'choose' not to. They suggest that this is due to disruption of a basal ganglia signal of the cost–reward relationship, which they term 'motor motivation'.
- 24 Patton JL, Stoykov ME, Kovic M, *et al.* Evaluation of robotic training forces that either enhance or reduce error in chronic hemiparetic stroke survivors. *Exp Brain Res* 2006; 168:368–383.
- 25 Scheidt RA, Stoeckmann T. Reach adaptation and final position control amid environmental uncertainty after stroke. *J Neurophysiol* 2007; 97:2824–2836.
- This is a study of hemiparetic stroke survivors making reaching movements in the face of perturbations. It is shown that these individuals still maintain the ability to adapt, though they do so less efficiently than controls. They also weighted errors from more recent reaches higher than did the controls.
- 26 Reisman DS, Wityk R, Silver K, *et al.* Locomotor adaptation on a split-belt treadmill can improve walking symmetry poststroke. *Brain* 2007; 130:1861–1872.
- This paper reports on a study of hemiparetic stroke survivors adapting their walking pattern on a split-belt treadmill. The important results are two-fold. First, they show that stroke survivors can adapt their locomotor pattern similar to that of controls. This is in contrast to cerebellar patients who cannot adapt. Second, stroke survivors can show after-effects from adaptation that normalizes step symmetry and timing of the walking pattern. This suggests that the nervous system is capable of generating a more normal walking pattern and raises the possibility that long-term learning through adaptation might be able to correct the faulty pattern.
- 27 Cothros N, Wong JD, Gribble PL. Are there distinct neural representations of object and limb dynamics? *Exp Brain Res* 2006; 173:689–697.
- 28 Kluzik J, Diedrichsen J, Shadmehr R, *et al.* Reach adaptation: what determines whether we learn an internal model of the tool or adapt the model of our arm? *J Neurophysiol* 2008 [Epub ahead of print].
- This study addressed whether reach adaptation to perturbations driven by a robot leads to after-effects that generalize to more natural 'free' reaches. The fundamental question is whether adapting with a device like a robot leads to calibration of an internal representation of the arm or of the robot. Results showed that patients only generalize about 40% of the adaptation with a robot to free space, suggesting that much of what is adapted is a representation tied to the robot. However, when perturbations generated by the robot are gradually and implicitly increased (versus immediately full strength) generalization improves to 60%. In sum, practice with a novel device like a robot results in formation of an internal model of the robot and produces a smaller change in the internal model of the patient's arm. However, gradual changes in the robot dynamics increase the extent to which the nervous system recalibrated the model of the patient's own arm.
- 29 Rossetti Y, Rode G, Pisella L, *et al.* Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature* 1998; 395:166–169.
- 30 Pisella L, Rode G, Farnè A, *et al.* Dissociated long lasting improvements of straight-ahead pointing and line bisection tasks in two hemineglect patients. *Neuropsychologia* 2002; 40:327–334.
- 31 Rode G, Pisella L, Rossetti Y, *et al.* Bottom-up transfer of sensory-motor plasticity to recovery of spatial cognition: visuomotor adaptation and spatial neglect. *Prog Brain Res* 2003; 142:273–287.
- 32 Doyon J, Benali H. Reorganization and plasticity in the adult brain during learning of motor skills. *Curr Opin Neurobiol* 2005; 15:161–167.
- 33 Kojima Y, Iwamoto Y, Yoshida K. Memory of learning facilitates saccadic adaptation in the monkey. *J Neurosci* 2004; 24:7531–7539.
- 34 Brashers-Krug T, Shadmehr R, Bizzi E. Consolidation in human motor memory. *Nature* 1996; 382:252–255.
- 35 Caithness G, Osu R, Bays P, *et al.* Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. *J Neurosci* 2004; 24:8662–8671.
- 36 Goedert KM, Willingham DB. Patterns of interference in sequence learning and prism adaptation inconsistent with the consolidation hypothesis. *Learn Mem* 2002; 9:279–292.
- 37 Bock O, Schneider S, Bloomberg J. Conditions for interference versus facilitation during sequential sensorimotor adaptation. *Exp Brain Res* 2001; 138:359–365.
- 38 Krakauer JW, Ghez C, Ghilardi MF. Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J Neurosci* 2005; 25:473–478.
- 39 Krakauer JW, Shadmehr R. Consolidation of motor memory. *Trends Neurosci* 2006; 29:58–64.

- 40 Richardson AG, Overduin SA, Valero-Cabré A, *et al.* Disruption of primary motor cortex before learning impairs memory of movement dynamics. *J Neurosci* 2006; 26:12466–12470.
- 41 Muellbacher W, Ziemann U, Wissel J, *et al.* Early consolidation in human primary motor cortex. *Nature* 2002; 415:640–644.
- 42 Baraduc P, Lang N, Rothwell JC, *et al.* Consolidation of dynamic motor learning is not disrupted by rTMS of primary motor cortex. *Curr Biol* 2004; 14:252–256.
- 43 Shemmell J, Riek S, Tresilian JR, *et al.* The role of the primary motor cortex during skill acquisition on a two-degrees-of-freedom movement task. *J Mot Behav* 2007; 39:29–39.