Motor learning and prediction in a variable environment
Paul R Davidson and Daniel M Wolpert

Traditional studies of motor learning and prediction have focused on how subjects perform a single task. Recent advances have been made in our understanding of motor learning and prediction by investigating the way we learn variable tasks, which change either predictably or unpredictably over time. Similarly, studies have examined how variability in our own movements affects motor learning.

Addresses
Sobell Dept of Motor Neuroscience and Movement Disorders, Institute of Neurology, University College London, Queen Square, London, WC1N 3BG, UK
e-mail: p.davidson@ieee.org

Abbreviations
MD   medio-dorsal thalamus

Introduction
In everyday life we are required to move about in a changing and often unpredictable environment. Despite these variations we remain able to achieve our behavioural goals with apparent ease. Motor control researchers have recently shown increasing interest in understanding how we learn to control our movements and predict the consequences of our actions in predictably and unpredictably varying environments. Computer controlled virtual environments, usually including a robotic manipulandum for force feedback, are often employed in this research as they allow experimenters to precisely control the parameters of their subject's mechanical and visual environment. When subjects are exposed to a new mechanical environment their movements are initially perturbed, but return to approximately their normal pattern after several hundred movements. Here, we review recent studies looking at motor learning and prediction.

Motor learning in an uncertain environment
Several studies have examined how we learn tasks whose parameters vary randomly over time. Takahashi et al. [1] asked subjects to make elbow flexion and extension movements against a viscous load, the strength of which was drawn randomly from a Gaussian distribution in each trial. In this randomly varying environment, subjects learned the average of the loads they experienced. Scheidt et al. [2•] confirmed that this was also true for planar reaching movements in which a velocity-dependent force field, of varying amplitude, was applied at the hand by a robotic manipulandum (by force field we mean a force that is related to the state of the hand). On the basis of a time-series analysis of performance, they showed that the subject's estimate of the expected force was based on the weighted average of performance over the previous few trials. Moreover, they examined trials in which the amplitude of the force field was drawn from a bimodal distribution, such that high and low forces were frequently experienced but moderate amplitudes (the mean) were experienced infrequently. In this situation, subjects tend to learn the mean rather than the most frequently experienced amplitude (the mode). In a related experiment, Witney et al. [3] examined the development of anticipatory responses. When one hand pulls on an object held in the other, the restraining hand generates an anticipatory increase in grip force, and thereby prevents the object from slipping. In the experiment performed by Witney et al., subjects held an object, whose properties were under computer control, between their hands. When the properties of the object were randomly changed between trials, the anticipatory modulation of grip force depended on the weighted average of the object's properties, as experienced over the previous three trials, with the weighting increasing for the most recent trials. These results suggest that in a randomly varying environment, a short-term averaging process underlies the representation of the task in motor working memory, and that learning may not represent the statistics of how the perturbation changes over a longer time scale.

Predictably varying environments
Adaptation to predictably varying environments has also been investigated. Karniel and Mussa-Ivaldi [4•] taught subjects, on separate days, to move in two different velocity-dependent force fields applied at the hand by a robotic manipulandum. Even after this experience, subjects were unable to move accurately when the same two fields alternated after each movement. This suggests that, although subjects can learn and maintain accuracy in both force fields [5], rapid switching in motor working memory is not possible. Wigmore et al. [6•] have found support for this in visuomotor learning of rotated visual feedback. They found that multiple visuomotor rotations seem to compete for the same working memory resources. These studies suggest that computational mechanisms which average across recent trials are used to learn both

predictable and randomly varying tasks, which explains why we cannot represent rapidly alternating environments.

Control strategies

There are two distinct strategies people might employ when learning novel dynamic tasks, such as moving while an external force acts on their hand. First, by learning the forces required to compensate for an externally imposed perturbation they might directly counteract the perturbing influence. Alternatively, by co-contracting muscles, they increase the stiffness of their arm and thereby reduce the displacement caused by an external force. When reaching in a predictable force field people tend to employ a low-stiffness strategy and learn to represent the compensatory forces [7,8]. Early in the process of learning the stiffness of the arm reduces systematically as these compensatory responses are learned [9•,10]. When manipulating an external object with internal degrees of freedom, such as a heavy mass attached to a spring, people also employ low-stiffness control [11]. In several situations, however, it is not possible to reliably predict the forces the hand will experience, and therefore compensation is difficult. For example, when drilling into a wall with a power drill, the aim is to maintain the drill bit perpendicular to the wall while applying an orthogonal force [12]. This situation is inherently unstable, in that any deviations from orthogonality lead to forces that destabilise the posture. In this situation the stiffness of the hand can be increased in all directions, thereby stabilising the system. Burdet *et al.* [13••] have used an analogous task in which the instability was present in only one direction (Figure 1). Subjects in this study had to reach from a starting point along a straight line towards a target. Any deviation of the hand during the movement was exacerbated by a force acting perpendicular to the line. They showed that subjects tailored the stiffness of the hand to match the requirements of the task, stiffening the hand only in the perpendicular direction. This is the first demonstration that stiffness can be controlled independently in different directions. Hence, it seems that we employ both high- and low-stiffness control strategies, with the high-stiffness control reducing the effect of any perturbations that a short-term averaging process cannot represent.

Several studies have investigated how learning a dynamic task (e.g. movement in a force field) affects a previously learned visuomotor task (e.g. a visual rotation). In some

Figure 1
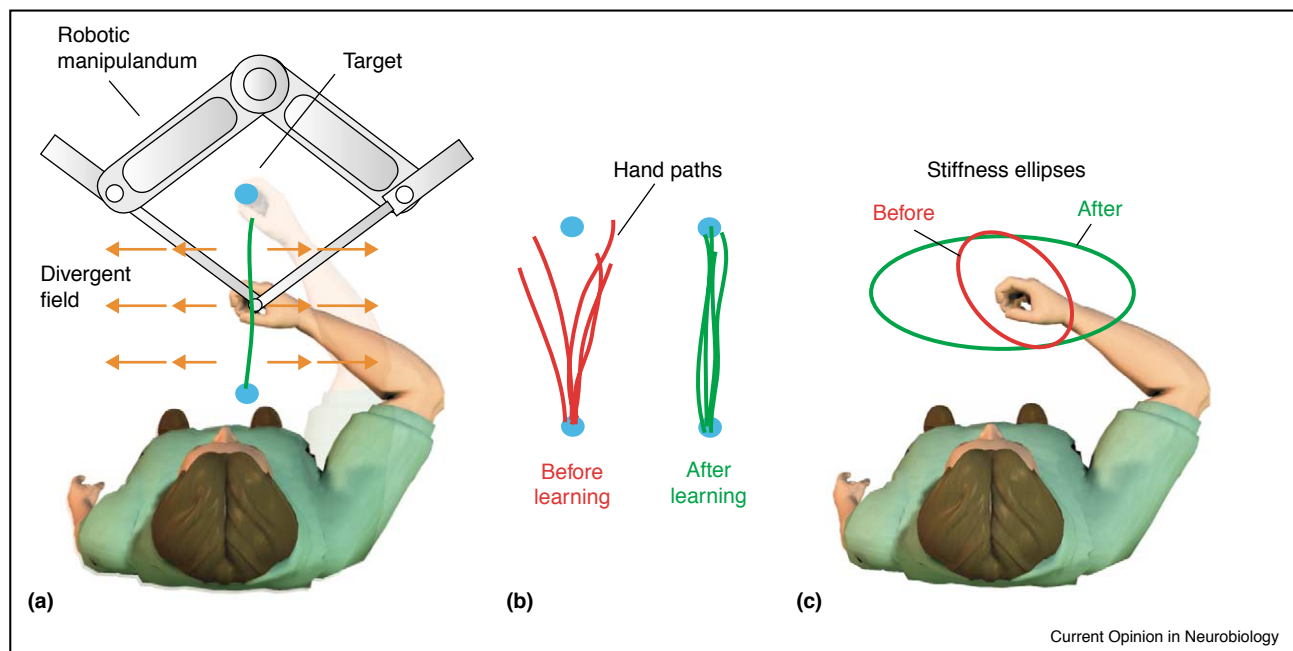
The CNS is able to increase the stiffness of the arm by co-contracting muscles during a movement. This strategy reduces the susceptibility of the arm to external force perturbations. A high-stiffness strategy reduces the need for complex neural representations of sensorimotor transformations, but at a cost of requiring the muscles to work harder. **(a)** In an experiment by Burdet *et al.* [13••], subjects were required to make reaching movements in a divergent field produced by a robotic manipulandum. The field is unstable as any deviation from a straight path will generate a force that acts in the same direction. **(b)** Initially, this caused the subject's hand paths to diverge from the target, but with practice, subjects learned to make straight movements. **(c)** The improvement was achieved by increasing the stiffness of the arm, but only in the direction of maximum instability. The stiffness ellipse represents restoring force to a step displacement of the hand in different directions. After learning, the stiffness ellipse is stretched in direction of the unstable force, indicating that performance was improved by increasing the stiffness of the arm, but only in the direction of maximum instability.

circumstances, we are able to learn an acceleration-dependent force-field without affecting a previously learned visuomotor rotation [14]. However, learning a position-dependent force field substantially interferes with a previously learned visuomotor rotation [15•]. The features that determine the extent to which a visuomotor and a dynamic task interfere are still not known.

Motor prediction

The ability to predict the future state of the motor system is thought to be essential for skilled movement because of the delays inherent in the sensorimotor system. Recent evidence has suggested that we predict the consequences of our motor commands and the behaviour of external objects to generate current estimates of the state of our body and the environment.

It has recently been shown that we are able to predict subtle variations in the dynamic state of our arms. Ariff et al. [16] hid subjects' arms from view and asked them to make reaching movements without visual feedback. They were asked to track the position of their unseen hand with their eyes. Subjects made saccadic movements to a location that predicted the position of their hand 196 ms in the future. A brief force pulse was then applied to the hand, thereby altering the state of the arm. After the pulse, saccades were suppressed for 100 ms, and then accurate predictive saccades re-emerged. This inhibition period may reflect the time taken to recompute an estimate of hand position. After the dynamics of the arm were altered by applying a novel velocity dependent force field, however, the subject's subsequent saccades were inaccurate. This suggests that subjects rely on an internal estimate of arm dynamics to generate their predictions.

The forces people apply with their fingers as they manipulate objects also show subtle variations consistent with access to internal predictions. Because of the configuration of the arm, the effective inertia at the hand varies with the direction of movement (inertial anisotropy). This variation in inertia is reflected in the fact that the initial acceleration of the hand is slower for high inertia directions (Figure 2). Flanagan et al. [17••] have shown that when sliding an object across a frictionless surface in different directions subjects vary the force they apply

Figure 2
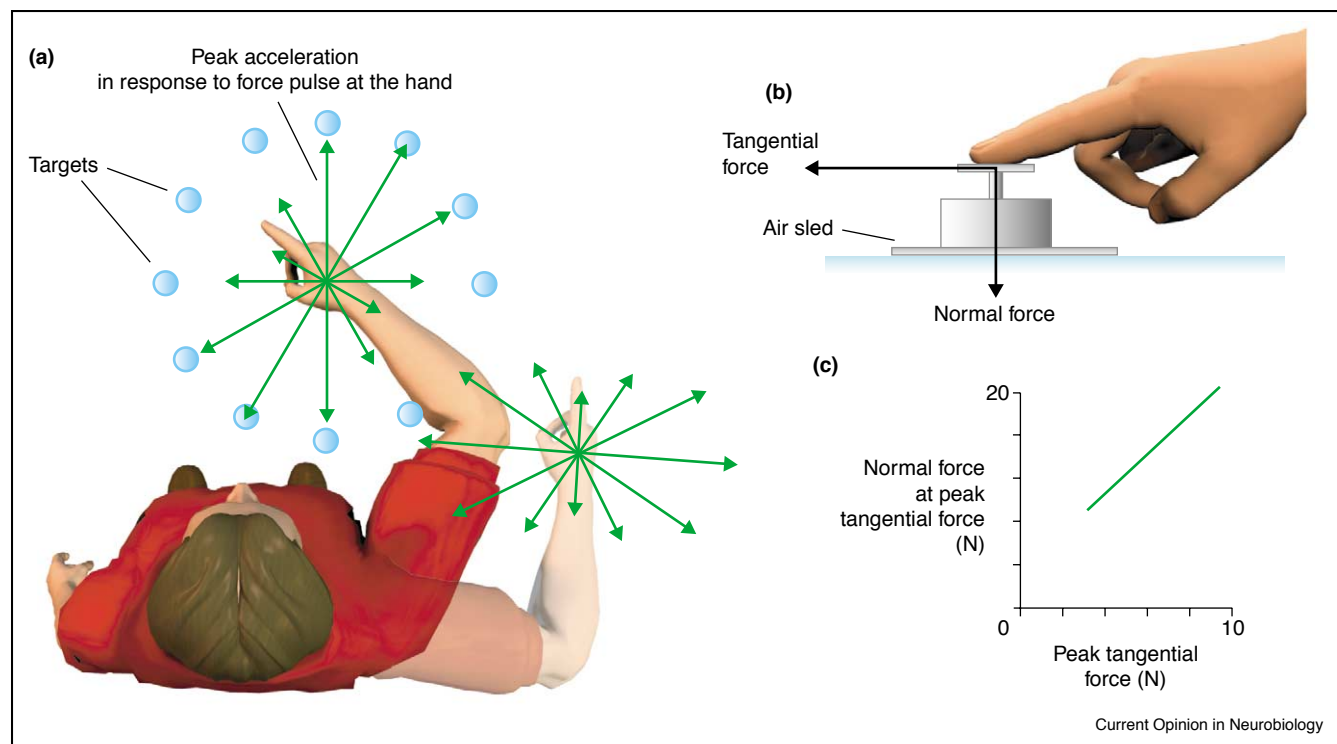
People are able to precisely predict the effects of directional variations in the inertia of their arm. **(a)** The peak acceleration of the hand (green arrows) in response to a force pulse varies with direction due to the inertial anisotropy of the arm. In an experiment by Flanagan et al. [17••], subjects pointed to targets that were arranged radially around the starting point. Pointing movements were made from two different initial arm positions. **(b)** An air-sled containing a force transducer was used to record the forces generated at the finger. **(c)** The normal (downward) force generated was precisely coordinated in anticipation of the tangential forces generated during the arm movement, regardless of starting posture. This was reflected in a strong positive correlation between the peak tangential force and the normal force generated at the same instant. Hence, the accelerative effects of differing effective inertia in each direction were accurately predicted by the motor system.

normal to the surface in anticipation of the direction-dependent change in initial hand acceleration. This indicates the presence of a predictive model that allows for the effects of anisotropic inertia. McIntyre *et al.* [18] have shown that predictive models are tuned for the effects of gravity. When catching a vertically falling ball, people normally generate accurately timed anticipatory responses to intercept the ball. During space travel, however, these anticipatory responses occur too early, indicating that the CNS employs an internal model of acceleration due to gravity, which is inappropriate in a zero gravity environment. As subjects spend more time in a zero gravity environment the anticipatory response slowly improves, but never reaches the performance that is achieved in terrestrial gravity.

Modelling the performance of subjects who were asked to balance a pole on their fingertip has also provided evidence for predictive models. Upon examining a variety of control schemes, Mehta and Schaal [19] concluded, through a process of elimination, that it was likely that a forward predictive model was employed. Such forward predictive models are thought to use a copy of the motor command to predict the consequences of an action. Good theoretical arguments have been put forward in favour of such a scheme of prediction, although neurophysiological evidence for such a process has emerged only recently. Sommer and Wurtz [20••] have suggested that medio-dorsal (MD) thalamic neurons carry a corollary discharge signal, from the superior colliculus to the frontal eye fields (FEF), that is used to update the estimate of eye position during saccades. The MD neurons fire before saccade onset, demonstrating that their activity is linked to the motor command and not the sensory feedback. When these neurons are inactivated by a local application of muscimol, the precision and velocity of a saccade to a single target is unaffected. However, in accordance with a failure to fully use the predictive mechanism, the accuracy of the second saccade of a double-step task shows biases that would be expected if the state of the eye were not fully updated.

Motor learning and consolidation
Several studies have examined memory consolidation after learning motor tasks. Memory consolidation is the process by which memory representations become increasingly robust with the passage of time. In the hours after learning a dynamic motor task, such as movement in a force field, progressive memory consolidation takes place [21,22]. Unlike the consolidation of perceptual skills and sequence learning [23•,24–26], this process does not require a period of sleep [27]. It was recently revealed that motor consolidation of a very simple speed task can be interrupted by performing repetitive transcranial magnetic stimulation over the primary motor cortex [28,29]. Consolidation of a dynamic learning task is well established, whereas it has recently been observed

that the process of consolidation does not occur after learning a visuomotor transformation or a movement sequence [30], but this could be because of their differing anatomical loci [31].

It is generally believed that subjects can learn tasks better with their dominant hand than with their non-dominant hand. Sainburg [32] has recently shown that the dominant hand has a clear advantage in learning novel inertial dynamic forces but that no advantage is observed when learning to compensate for a visuomotor rotation. This observation led to the 'dynamic dominance hypothesis' of handedness, which proposes that differences in dominant and non-dominant limb performance arise from a differential ability to control limb dynamics. Despite clear differences in the ability to learn dynamics, there is evidence of generalisation of learned dynamics between hands, at least from the dominant to the non-dominant hand [33].

Optimal control
Most movement tasks can be achieved using many different joint configurations, levels of co-contraction and so on. Several studies have sought to understand why certain motor patterns are preferred to others (stereotypy). These studies place motor learning within an optimal control framework, in which a task is associated with a cost, for example, the energy consumed or the time taken to complete the task. Planning or learning can be considered to be part of producing the movement that best minimises the cost. For example, for arm movements, costs that penalise the lack of smoothness, by penalising either the rate of change of acceleration of the hand (jerk) [34] or the rate of change of torque at the joints, have been successful for modelling human movements. Recently, costs that take into account the variability of the motor command have been developed. Force production shows signal-dependent noise, which is variability in force with a constant coefficient of variation. Harris and Wolpert [35] and Kitazawa [36] suggested that controlling the statistics of movement in the presence of a signal that depends on the motor command is a major determinant of motor planning. Recently, Todorov and Jordan [37••] have shown that optimal feedback control in the presence of signal-dependent noise may form a general strategy for movement production. This model suggests that rather than forming a desired trajectory, the motor system may use optimal feedback control to deal with deviations that interfere with the task goal.

Conclusions
We have reviewed recent advances in understanding motor learning and prediction. Progress has been made in understanding the effects on movement of a mechanical environment that varies both predictably and unpredictably. Our ability to predict the consequences of our own motor commands and the behaviour of external

objects is also being revealed in increasing detail. Although we have some partial answers the coming years should elucidate which motor tasks lead to competition in motor working memory, and whether there are multiple motor working memory systems. This work should also identify the common and distinct elements between motor learning and other forms of learning (e.g. perceptual). Finally, a unifying perspective should emerge which can tie together planning, prediction, control and learning into one framework.

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

1. Takahashi CD, Scheidt RA, Reinkensmeyer DJ: **Impedance control and internal model formation when reaching in a randomly varying dynamical environment**. *J Neurophysiol* 2001, **86**:1047-1051.

2. Scheidt RA, Dingwell JB, Mussa-Ivaldi FA: **Learning to move amid**
 • **uncertainty**. *J Neurophysiol* 2001, **86**:971-985.
During force-field learning, in which the force amplitude varied from movement to movement, subjects learned to prepare for the mean field experienced over the previous few movements. This implies that only short-term memory is used for motor adaptation. The same pattern was observed when the field amplitude for each trial was drawn from a strongly bimodal distribution.

3. Witney AG, Vetter P, Wolpert DM: **The influence of previous experience on predictive motor control**. *Neuroreport* 2001, **12**:649-653.

4. Karniel A, Mussa-Ivaldi FA: **Does the motor control system use**
 • **multiple models and context switching to cope with a variable environment?** *Exp Brain Res* 2002, **143**:520-524.
This paper investigates our ability to form, and then use, memories of multiple force fields. Subjects learned to reach in two force-fields that acted in opposite directions, perpendicular to the direction of hand movement. In the control condition, the fields alternated after every trial and very little learning was observed. On the following day, the subjects returned and learned the rightward field only. Twenty-four hours later they returned and learned to reach in the leftward field. Then, after 24 h, subjects were re-tested with alternating fields as in the control condition. Despite this, subjects were unable use their knowledge of the two force fields to improve their performance in the alternating condition.

5. Bhushan N, Shadmehr R: **Computational nature of human adaptive control during learning of reaching movements in force fields**. *Biol Cybern* 1999, **81**:39-60.

6. Wigmore V, Tong C, Flanagan JR: **Visuomotor rotations of**
 • **varying size and direction compete for a single internal model in motor working memory**. *J Exp Psychol Hum Percept Perform* 2002, **28**:447-457.
This study shows that multiple visuomotor rotations compete for the same working memory resources. Subjects learned a −30° rotation followed immediately by second rotation of either +30°, +60° or −60°. The following day they were re-tested on the original −30° rotation. Performance on the second day was consistent with subjects having consolidated the second rotation, with little memory of the rotation first experienced.

7. Thoroughman KA, Shadmehr R: **Electromyographic correlates of learning an internal model of reaching movements**. *J Neurosci* 1999, **19**:8573-8588.

8. Cohn JV, DiZio P, Lackner JR: **Reaching during virtual rotation: context specific compensations for expected coriolis forces**. *J Neurophysiol* 2000, **83**:3230-3240.

9. Wang T, Dordevic GS, Shadmehr R: **Learning the dynamics of**
 • **reaching movements results in the modification of arm impedance and long-latency perturbation responses**. *Biol Cybern* 2001, **85**:437-448.
The authors show that when learning to make arm movements in a novel force field, the sensorimotor feedback pathway is modified in parallel with the feed-forward pathway. A non-linear approach is used to approximate the impedance of the arm. The authors note that the hand impedance alters after subjects learn a new field and appears to be tuned specifically to counter the effects of the new field.

10. Nezafat R, Shadmehr R, Holcomb HH: **Long-term adaptation to dynamics of reaching movements: a PET study**. *Exp Brain Res* 2001, **140**:66-76.

11. Dingwell JB, Mah CD, Mussa-Ivaldi FA: **Manipulating objects with internal degrees of freedom: evidence for model-based control**. *J Neurophysiol* 2002, **88**:222-235.

12. Rancourt D, Hogan N: **Stability in force-production tasks**. *J Mot Behav* 2001, **33**:193-204.

13. Burdet E, Osu R, Franklin DW, Milner TE, Kawato M: **The central**
 •• **nervous system stabilizes unstable dynamics by learning optimal impedance**. *Nature* 2001, **414**:446-449.
The authors show that subjects adapt to an unstable force field by increasing the stiffness of their arm selectively in the direction of instability. This approach is more energy efficient than a generalised increase in limb stiffness.

14. Krakauer JW, Ghilardi MF, Ghez C: **Independent learning of internal models for kinematic and dynamic control of reaching**. *Nat Neurosci* 1999, **2**:1026-1031.

15. Tong C, Wolpert DM, Flanagan JR: **Kinematics and dynamics are**
 • **not represented independently in motor working memory: evidence from an interference study**. *J Neurosci* 2002, **22**:1108-1113.
Using a paradigm similar to that presented by Burdet *et al.* [13••], the authors show that a dynamic field can interfere with consolidation of a visuomotor rotation in some circumstances. Subjects learned a visuomotor rotation followed by a position-dependant rotary force field. Subjects were then re-tested on the same visuomotor rotation on the following day when their performance was impaired compared to the control group.

16. Ariff G, Donchin O, Nanayakkara T, Shadmehr R: **A real-time state predictor in motor control: study of saccadic eye movements during unseen reaching movements**. *J Neurosci* 2002, **22**:7721-7729.

17. Flanagan JR, Lolley S: **The inertial anisotropy of the arm is**
 •• **accurately predicted during movement planning**. *J Neurosci* 2001, **21**:1361-1369.
The authors show that the CNS accurately predicts direction-dependant changes in hand acceleration caused by the anisotropic inertia of the arm. Subjects slide an object across a frictionless surface to radially located targets. The force they apply to the object is accurately coordinated in anticipation of changes in tangential force caused by hand acceleration. The normal force remains accurate across movement directions and arm postures.

18. McIntyre J, Zago M, Berthoz A, Lacquaniti F: **Does the brain model Newton's laws?** *Nat Neurosci* 2001, **4**:693-694.

19. Mehta B, Schaal S: **Forward models in visuomotor control**. *J Neurophysiol* 2002, **88**:942-953.

20. Sommer MA, Wurtz RH: **A pathway in primate brain for internal**
 •• **monitoring of movements**. *Science* 2002, **296**:1480-1482.
The authors of this paper use a double saccade task to identify a possible pathway for corollary discharge, or efference copy, in the brain. The pathway leads from the superior colliculus to the frontal eye fields via the mediodorsal thalamus (MD), and was shown to carry information that correlated with the motor command for saccadic eye movement. Importantly, interruption of the pathway caused deficits consistent with the loss of corollary discharge: the pathway appears to carry information about a movement but is not directly involved in generating that movement.

21. Brashers-Krug T, Shadmehr R, Bizzo E: **Consolidation in human motor memory**. *Nature* 1996, **382**:252-255.

22. Shadmehr R, Brashers-Krug T: **Functional stages in the formation of human long-term motor memory**. *J Neurosci* 1997, **17**:409-419.

23. Walker MP, Brakefield T, Morgan A, Hobson JA, Stickgold R:
 • **Practice with sleep makes perfect: sleep-dependent motor skill learning**. *Neuron* 2002, **35**:205-211.

After learning a five-key-press movement sequence, a 20% increase in speed without loss of accuracy was observed after a night of sleep. In contrast, there was no significant improvement in speed after the same period spent awake. Hence, this paper provides evidence that sleep facilitates motor-sequence learning. Improved performance strongly correlated with the amount of late non-REM sleep obtained by the subjects.

24. Stickgold R, Hobson JA, Fosse R, Fosse M: **Sleep, learning, and dreams: off-line memory reprocessing**. *Science* 2001, **294**:1052-1057.

25. Fischer S, Hallschmid M, Elsner AL, Born J: **Sleep forms memory for finger skills**. *Proc Natl Acad Sci USA* 2002, **99**:11987-11991.

26. Maquet P: **The role of sleep in learning and memory**. *Science* 2001, **294**:1048-1052.

27. Donchin O, Sawaki L, Madupu G, Cohen LG, Shadmehr R: **Mechanisms influencing acquisition and recall of motor memories**. *J Neurophysiol* 2002, **88**:2114-2123.

28. Muellbacher W, Ziemann U, Boroojerdi B, Cohen L, Hallett M: **Role of the human motor cortex in rapid motor learning**. *Exp Brain Res* 2001, **136**:431-438.

29. Muellbacher W, Ziemann U, Wissel J, Dang N, Kofler M, Facchini S, Boroojerdi B, Poewe W, Hallett M: **Early consolidation in human primary motor cortex**. *Nature* 2002, **415**:640-644.

30. Goedert KM, Willingham DB: **Patterns of interference in sequence learning and prism adaptation inconsistent with the consolidation hypothesis**. *Learn Mem* 2002, **9**:279-292.

31. Ghilardi M, Ghez C, Dhawan V, Moeller J, Mentis M, Nakamura T, Antonini A, Eidelberg D: **Patterns of regional brain activation associated with different forms of motor learning**. *Brain Res* 2000, **871**:127-145.

32. Sainburg RL: **Evidence for a dynamic-dominance hypothesis of handedness**. *Exp Brain Res* 2002, **142**:241-258.

33. Criscimagna-Hemminger SE, Donchin O, Shadmehr R: **Learned dynamics of reaching movements generalize from dominant to non-dominant arm**. *J Neurophysiol* 2003, **89**:168-176.

34. Richardson MJ, Flash T: **Comparing smooth arm movements with the two-thirds power law and the related segmented-control hypothesis**. *J Neurosci* 2002, **22**:8201-8211.

35. Harris CM, Wolpert DM: **Signal-dependent noise determines motor planning**. *Nature* 1998, **394**:780-784. [See also 'News and Views' pages 725-726.]

36. Kitazawa S: **Optimization of goal-directed movements in the cerebellum: a random walk hypothesis**. *Neurosci Res* 2002, **43**:289-294.

37. Todorov E, Jordan MI: **Optimal feedback control as a theory of**
•• **motor coordination**. *Nat Neurosci* 2002, **5**:1226-1235.
Here, the authors propose a comprehensive theory of coordination that is based on a stochastic optimal feedback control framework. The authors demonstrate that the optimal control strategy in the face of uncertainty is to allow variability in redundant dimensions to go uncorrected. Only the deviations that actually interfere with task goals are actively corrected. Experimental results from a wide variety of tasks are also presented in support of their theory.