The Neural Basis of Motor-Skill Learning

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Abstract

Recent work indicates that motor-skill learning is supported by four processes: a strategic process that selects new goals of what to change in the environment, a perceptual-motor integration process that adjusts to new relationships between environmental stimuli and the appropriate motor response, a sequencing process that learns sequences of motor acts, and a dynamic process that learns new patterns of muscle activations. These four processes can operate in one of two modes: an unconscious mode, in which one is aware only of the goal of the movement, or a conscious mode, in which one consciously controls detailed aspects of the movement. This article provides an overview of these four processes and two modes, and describes their neural bases.

Keywords

motor skill; learning; motor control

If motor movements could not be performed more quickly and accurately with practice, getting dressed each morning would be a time-consuming affair, and driving to one's office on a highway full of novice motorists would provide more thrills than most of us want at an early hour. In the past 10 years, a great deal has been discovered about the anatomic structures that support motor-skill learning. A key result has been the description of different motor-skill functions subserved by different brain areas. This article provides an overview of some of these findings. Given the space restrictions, this article focuses on my own point of view, specifically, on a theory of motor-skill learning I have recently proposed (Willingham, 1998). More ecumenical reviews are available (Salmon & Butters, 1995).

FOUR PROCESSES SUPPORTING MOTOR-SKILL LEARNING

Motor-skill learning should be differentiated from motor control. Motor control refers to the processes that support the planning and execution of movements. Motor-skill learning refers to the increasing spatial and temporal accuracy of movements with practice. Recently, a number of researchers have proposed that motor-skill processes may grow directly out of motor-control processes; in other words, motor skill may be nothing more or less than the increasingly efficient operation of motor-control processes.

Figure 1 shows four hypothetical processes that support motor control. To make a movement, the actor[2] (a) selects a goal that something in the environment be changed, (b) selects spatial targets for movement that will achieve the goal, (c) sequences the spatial targets, and (d) translates the sequence of spatial targets into a pattern of muscle activity. How might these processes also support motor-skill learning?

In the first motor-control process, the actor selects the environmental goal of the movement. This process can support motor-skill learning through the selection of successively more effective goals. This function corresponds closely with the everyday use of the word *strategy*, and hence this process is called *strategic*. For example, a bowler faced with a difficult split may try to make the 10 pin strike the 7 pin.

In the second motor-control process, the actor selects spatial targets for movements that will achieve the environmental goal. This process is called *perceptual-motor integration*. The environmental goal is selected in allocentric space (i.e., a coordinate system in which objects are located relative to one another), but the target for movement is selected in egocentric space (i.e., a coordinate system anchored on a part of the body). Allocentric space depends on vision, and egocentric space depends on proprioception (information about the position of the body that comes from receptors in the muscles, tendons, joints, and skin), so learning becomes necessary when the relationship between them is changed. For example, spectacles made from wedge prisms will misalign vision and proprioception, making motor movements quite inaccurate, but movements improve with practice. Other, less disruptive changes also require learning (e.g., the translation between screen locations and mouse locations for someone using a computer).

The third motor-control process sequences spatial targets for movement. Learning supported by this *sequencing* process occurs when the actor must make the same sequence of movements repeatedly. For example, a tennis player perfecting a serve attempts to make the same sequence of movements each time. Many laboratory tasks psychologists use in their experi-

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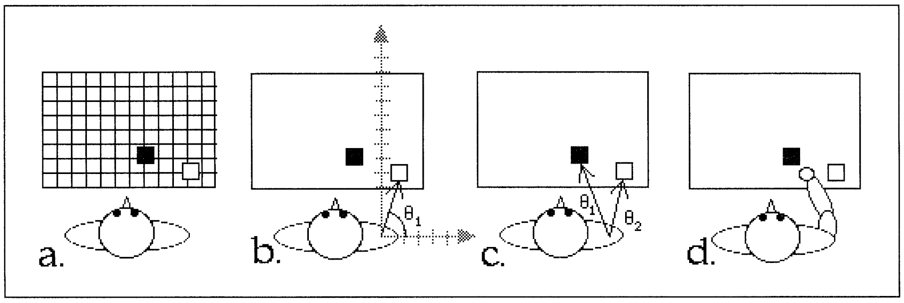

Fig. 1. Four processes of motor control. In the strategic process (a), the actor decides to move a drinking glass (filled square) to a new location (empty square). The spatial locations are described in allocentric space (i.e., relative to the table). In perceptual-motor integration (b), the spatial locations are translated into egocentric space, in this case, relative to the location of the shoulder. In the sequencing process (c), the two spatial locations are sequenced, to ensure that the current location of the glass is reached first, and then the goal location of the glass. Finally, in the dynamic process (d), the spatial targets are translated into a pattern of muscle activation to move the hand to the targets.

ments call for a sequence of movements to be repeated. For example, many tracking tasks[3] require subjects to keep a cursor on a target that moves in a repeating pattern.

The fourth process, called *dynamic,* translates the sequence of egocentric spatial targets into a pattern of muscle activation. This process could support skill learning when the relationship between egocentric space and muscle movements is poorly represented (e.g., fine movements made with the nonpreferred hand) or when the relationship changes (e.g., because of disfigurement or normal development). This form of motor learning has been little studied.

These four processes that support motor control are summarized in Table 1.

UNCONSCIOUS AND CONSCIOUS MODES OF MOTOR CONTROL AND MOTOR SKILL

I have proposed that there are two modes in which these four processes can operate, and these

Table 1. *The processes that support motor control*

Process	Function in motor control	Mechanism of improvement in motor-skill acquisition	Example	Anatomic locus
Strategic	Selects goal of movement in environmental coordinates	Select more effective environmental goals	Hit a lob when opponent rushes the net	Dorsolateral frontal cortex
Perceptual-motor integration	Selects spatial target or targets for movement that will fulfill environmental goal; represented in egocentric space	Learning a new relationship between environmental and egocentric space because of a change in vision or proprioception, or an incompatible stimulus-response mapping	Use a racquet to hit a ball instead of one's hand	Premotor cortex, posterior parietal cortex
Sequencing	Orders spatial targets in the correct sequence	Learning a repeating sequence when the same movement is made repeatedly	Stereotyping the movements for a tennis serve	Basal ganglia, supplementary motor cortex
Dynamic	Translates egocentric spatial targets and a pattern of muscle firing	Learning a new relationship between egocentric targets and the pattern of muscle firing necessary to move the effector to the spatial target	Learning fine coordination with nonpreferred hand	Spinal interneurons

two modes apply to both motor control and motor skill. In the *unconscious mode,* the actor is conscious only of setting the environmental goal—for example, of wanting to move a glass from one location on a table to another. The other processes operate outside of consciousness. In the *conscious mode,* the strategic process not only selects the environmental goal, but also selects and sequences the spatial targets for movement. Under typical circumstances, the actor employs the unconscious mode and is conscious only of wanting the glass moved from one location to the other. However, the actor can also use the conscious mode and consciously consider the exact location in which the glass is to be grasped and the sequence of movements necessary to move the glass. When the conscious mode is used, the output of the strategic process replaces the output of the sequencing and perceptual-motor integration processes.

This use of the conscious mode can play a role in motor-skill learning. In the prism-spectacles task, wedge prisms shift the visual world (often 30° to the right), and the subject must point to visual targets. The subject may simply make reaching movements without any attempt to consciously counteract the effects of the spectacles. Such movements are made in the unconscious mode, and although performance will initially be quite inaccurate, performance will improve with training because of learning in the perceptual-motor integration process. The subject may, however, obtain explicit, conscious knowledge of the effect of the spectacles. The subject can then use the conscious mode to select a target for movement that corrects for the distorting effects of the prisms. In this case, performance will improve much more quickly. Sequencing tasks, too, may be learned wholly unconsciously, or more rapidly in the conscious mode.

BRAIN BASIS OF MOTOR-SKILL LEARNING

Recent evidence shows that the four processes described have distinct neural bases. Readers may wish to refer to Figure 2 for an illustration showing some of these locations.

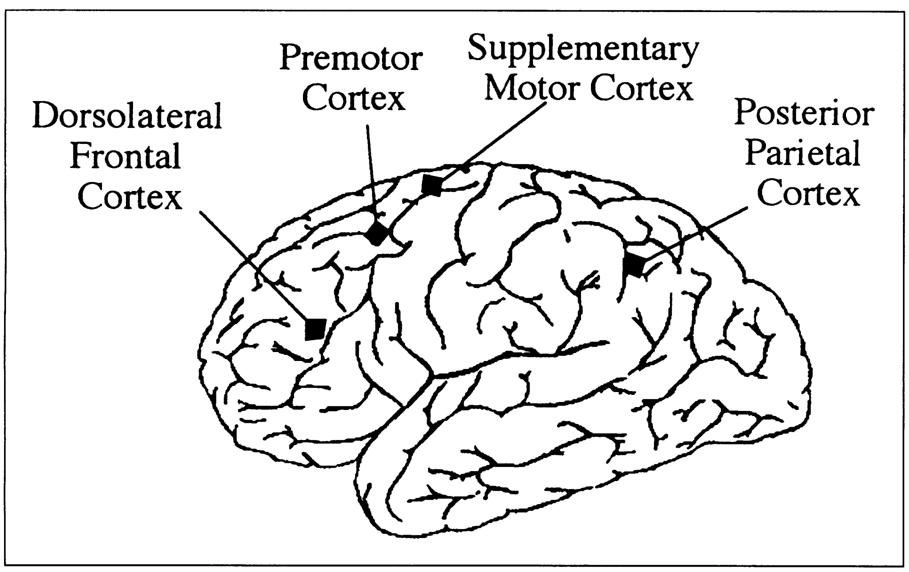

Fig. 2. Brain locations associated with motor-skill learning. See the text for details.

The dorsolateral frontal cortex has been implicated in the strategic process. Positron emission tomography studies show activation in this region when subjects must select a movement to execute, relative to a condition in which the stimulus specifies which movement to make. Further, patients with frontal lobe lesions have problems in selecting actions, although the deficit can take different forms: Some patients select very few actions (i.e., they are content to simply sit for long periods wherever they are placed); others select inappropriate environmental goals (e.g., trying to open a can by pounding it with a can-opener); others repeatedly select the same environmental goal (e.g., repeatedly beating an egg and not progressing to the next step in baking a cake).

The perceptual-motor integration process can be localized to posterior parietal cortex and premotor cortex. Its locus has been examined using the prism-spectacles task, even though learning in this task may entail both perceptual-motor integration and strategic learning. Perceptual-motor integration learning may be assessed in isolation by a transfer task that measures aftereffects: If subjects are trained with the prism spectacles and then asked to point straight in front of the nose with eyes closed (so that visual feedback cannot be used), they point in the direction opposite to the prism transformation (e.g., if the spectacles shifted the visual world to the right, they point to the left). This bias occurs because training with the prism spectacles changes proprioception—subjects feel that they are pointing straight ahead. Functional imaging studies using positron emission tomography and magnetic resonance imaging show that the posterior parietal cortex is a critical site of learning in the prism-spectacle task (Clower et al., 1996), and other studies show that patients with damage that spares pos-

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terior parietal cortex and premotor cortex (such as patients with Alzheimer's disease, Huntington's disease, and Parkinson's disease) show normal aftereffects in this task. These patients also successfully learn new relationships between stimuli and the appropriate motor responses (e.g., learning to use a computer mouse or joystick).

Learning motor sequences appears to rely on the basal ganglia and supplementary motor cortex. Patients with basal ganglia abnormalities due to Huntington's disease or Parkinson's disease show impaired learning of tracking tasks that use a target moving in a repeating sequence, but they are able to learn tracking tasks normally if the targets move randomly (such tasks do not require sequence learning). Patients with lesions that spare the basal ganglia (e.g., patients with Alzheimer's disease) show normal learning of sequencing tasks. Functional imaging studies also implicate the basal ganglia and supplementary motor area in sequence-learning tasks. These anatomic areas are consistently activated in neurologically intact subjects who learn the serial response time task[4] or a tracking task in which the target moves in a repeating sequence. In one recent study (Rauch et al., 1997), the amount of activation in the putamen (one structure in the basal ganglia) was correlated with the amount of sequence learning subjects showed in the serial response time task.

As noted earlier, there has been virtually no work examining the neural basis of dynamic learning, but there is evidence indicating the neural basis of the dynamic control process is in pools of interneurons[5] in the spinal cord (see Bizzi, Giszter, Loeb, Mussa-Ivaldi, & Saltiel, 1995). Thus, although it is plausible that spinal interneurons may also support dynamic learning, the issue has not yet been investigated.

BRAIN BASIS OF CONSCIOUS AND UNCONSCIOUS LEARNING

The strategic process selects environmental goals for movement and sequences targets for movements when subjects respond in the conscious mode. There is some evidence that the latter function is supported by the dorsolateral frontal cortex. As noted earlier, the conscious mode can be used to implement a strategy in learning to adjust to prism spectacles; one can select a target for pointing that "looks wrong" but that adjusts for the effect of the prisms. Patients with frontal lobe lesions are impaired in adjusting to prism spectacles, perhaps because normal subjects spontaneously develop conscious strategies for movement, whereas frontal patients do not.

In a number of functional imaging experiments, subjects learned to tap a particular sequence of finger-to-thumb movements. If the sequence was learned consciously, activations associated with learning were observed in prefrontal cortex (which includes the dorsolateral frontal cortex and other cortical areas), as well as supplementary motor and premotor cortices. If the sequence was learned unconsciously, little or no activation in prefrontal cortex occurred (see Willingham, 1998, for a review). The frontal activation decreased with practice, and the decrease began when subjects reported that they no longer needed to internally count the finger taps (Seitz, Roland, Bohm, Greitz, & Stone-Elander, 1990). But if subjects were then asked to attend to the process of producing this very well learned sequence of finger movements, the frontal activity returned (Jueptner et al., 1997). These results strongly suggest that the conscious mode of control is supported by the dorsolateral frontal cortex.

Learning continues in the unconscious processes all the while that the conscious mode is engaged and controlling movement. Thus, the subject may consciously control a sequence of movements, but with sufficient practice, this conscious control becomes unnecessary because the unconscious sequencing process will have learned the sequence. This interaction of the two processes would account for the decreasing attentional demands observed with practice and the development of automaticity. A recent behavioral study supports this idea. Goedert-Eschmann and I (Willingham & Goedert-Eschmann, 1999) trained subjects in the serial response time task. Some subjects learned the sequence consciously, and some unconsciously. Next, all subjects were told that the stimuli would appear randomly, when in fact the sequence occasionally appeared in an otherwise random trial block. None of the subjects noticed the occasional appearance of the trained pattern, and all subjects showed equivalent unconscious knowledge of the pattern. The implication is that subjects who had learned the sequence via the conscious mode had simultaneously learned it unconsciously.

AREAS OF FUTURE WORK

The basic architecture of the neurological substrate of motor-skill learning is emerging. This architecture is composed of a number of anatomically distinct processes, each performing a different function for motor-skill acquisition, and each rooted in processes of motor control. Several outstanding questions remain.

First, there are other brain structures that appear to contribute to motor-skill learning, but their function is not yet known. For example, functional imaging studies frequently show activation in the primary motor cortex, but its role in skill learning is not well understood. It may simply show activation because of its connections to the supplementary motor and premotor cortices, or it may make an independent contribution to motor skill. The role of somatosensory cortex (which is crucial to proprioception) also remains obscure. The theory described here holds that proprioception is critical because of its role in determining egocentric spatial location, and indeed there are data showing impaired motor-skill learning in the face of proprioceptive loss, but this work has only begun.

A second area of future work concerns features of movement, specifically, force and timing. All of the work described in this article has been concerned with the spatial aspect of skills. In most tasks, timing information is confounded with spatial information if it is present at all, but some recent work shows that subjects can learn timing information on its own. It is well established that the cerebellum plays a crucial role in timing in motor control, so one might expect that the cerebellum is important for learning temporal information in motor-skill tasks. Skill involved in force production has also been understudied.

A third area of future work may be clarification of the mechanisms within each of the putative processes outlined here. I have proposed that the basal ganglia and supplementary motor cortex support motor-skill learning—but by what mechanism? How are sequences learned? The work described shows the power of a neuropsychological analysis in outlining the broad framework of a model. The detailed mechanisms within each of the processes remain to be described.

Recommended Reading

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Notes

1. Address correspondence to Daniel B. Willingham, Department of Psychology, 102 Gilmer Hall, University of Virginia, Charlottesville, VA 22903.

2. "Actor" refers to a person executing a motor act.

3. In a tracking task, a target moves and the subject pursues it. Typically, the task is administered on a computer. The target is a circle moving on a screen, and the subject attempts to keep a computer cursor on the target by manipulating a joystick or computer mouse.

4. In the serial response time task, the subject sees four squares arrayed horizontally on a computer screen and rests the index and middle fingers of each hand on response keys. One square becomes filled in black, and the subject must press the key corresponding to that square, whereupon the square becomes white again, and a new square is filled in black. The squares become filled in a repeating sequence of spatial positions, although the subject is not told this. In a typical experiment, the sequence is 12 units long, and nothing marks the beginning or end of the sequence, so it may appear to the subject to be a random stream of stimuli. Although many subjects remain unaware that the stimuli are sequenced, steadily decreasing response times nevertheless show that they have learned the sequence unconsciously.

5. Interneurons connect with motoneurons, which in turn directly drive muscle activity.

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