# A Neuropsychological Theory of Motor Skill Learning

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This article describes a neuropsychological theory of motor skill learning that is based on the idea that learning grows directly out of motor control processes. Three motor control processes may be tuned to specific tasks, thereby improving performance: selecting spatial targets for movement, sequencing these targets, and transforming them into muscle commands. These processes operate outside of awareness. A 4th, conscious process can improve performance in either of 2 ways: by selecting more effective goals of what should be changed in the environment or by selecting and sequencing spatial targets. The theory accounts for patterns of impairment of motor skill learning in patient populations and for learning-related changes in activity in functional imaging studies. It also makes a number of predictions about the purely cognitive, including accounts of mental practice, the representation of motor skill, and the interaction of conscious and unconscious processes in motor skill learning.

Motor control refers to the planning and execution of movements; motor skill learning refers to the increasing spatial and temporal accuracy of movements with practice. Although considerable progress has been made in understanding the neural basis of motor control (e.g., Bizzi, Giszter, Loeb, Mussa-Ivaldi, & Saltiel, 1995; Georgopoulos, Kalaska, & Massey, 1981), the neural basis of motor skill learning has remained elusive. But motor skill learning is fundamental to human activity and so is worthy of close attention. It would be a strange, cruel world without motor skill learning: Automobile drivers would get behind the wheel as if for the first time every day; there would be no virtuosic athletic and artistic performances to watch; and tying one's shoes in the morning would require minutes of intense concentration.

There has been a noticeable increase in the number of studies examining the neural basis of motor skill learning over the past 10 years, which has afforded greater opportunity for integrative theory. But these data have also led to some confusion, because a large number of brain areas have been implicated in motor skill learning, as shown in Table 1. It seems probable that each of these areas contributes a different computation to motor skill learning, given the localization of separate computations found in other functional systems such as perception (Ungerleider & Mishkin, 1982), attention (Posner & Petersen, 1990), and memory (Squire, 1992). But what are the computations that underlie motor skill learning?

The theory proposed here suggests that motor skill learning grows directly out of motor control processes. This theory posits that learning occurs as one or more of four hypothetical processes that support motor control become tuned to a particular task, thus operating more efficiently. The theory also proposes a second mechanism by which motor skill learning may occur: Conscious, strategic processes may substitute for some of these motor control processes, leading to improved performance.

The purview of the theory is primarily neuropsychological. The goal is to specify not only the computation that each of the brain areas listed in Table 1 contributes, but also how these computations work together in the acquisition of complex motor skills. Because it specifies processes and representations that these brain areas utilize, the theory also accounts for data and makes new predictions in the cognitive domain, incorporating diverse phenomena such as mental practice and "choking under pressure."

The domain of the theory is the learning of new motor skills, not those skills that are likely to be in large measure innate (e.g., locomotion, mastication, the vestibulo-occular response), because the mechanism of learning in such skills may be qualitatively different. Further, the theory currently accounts only for the development of spatial accuracy in motor skill. A complete theory of motor skill learning will account for temporal accuracy as well, and future versions of the theory will account for temporal learning phenomena.

The article is divided into five sections. The first describes three principles of motor control and a basic architecture of motor control based on these three principles. The second shows how the architecture based on these three principles can also support motor skill learning. The final three sections describe predictions and data relevant to the three principles of the proposed motor skill learning theory.

## Three Principles of Motor Control

The present theory proposes that motor skill learning is a direct outgrowth of motor control processes. This relationship between motor control and motor skill learning is the basis of the theory's name, COBALT (control-based learning theory). The theory applies three principles of motor control to motor skill learning: these three principles constitute the background assumptions of COBALT. The *neural separability principle* proposes that different cognitive components of motor control are

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## Table 1

Brain Areas Implicated in Motor Skill Learning in Humans and Earliest Citations to Emphasize Their Importance to Motor Skill Acquisition

Structure or cortical area	Investigator			
Primary motor cortex	Seitz et al., 1990			
Supplementary motor area	Grafton et al., 1992			
Premotor cortex	Petrides, 1985			
Prefrontal cortex	Canavan et al., 1990			
Striatum	Heindel et al., 1989			
Cerebellum	Weiner et al., 1983			
Somatosensory cortex	Sakamoto et al., 1989			
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subserved by anatomically distinct parts of the brain. The disparate representation principle proposes that these different cognitive components utilize different forms of representation. The dual mode principle proposes that motor acts can be executed either in a conscious, effortful mode or in an unconscious, automatic mode.

The neural separability principle proposes that separate processes with distinct neural bases underlie motor control, as shown in Figure 1. The first is a strategic process, based in the dorsolateral frontal cortex, that identifies a goal (i.e., a change to the environment to be brought about). For example, a tennis player may generate a goal that a serve be hit so that the ball lands in the back right corner of the service box. The second process is a perceptual-motor integration process, based in the posterior parietal lobe and premotor cortex, that selects targets for movement. Because the tennis ball is hit with a racquet and not with part of the body, the tennis player must calculate where to move his or her hand so that the hand movements result in hitting the ball with the head of the racquet. The third process is a sequencing process, based in the supplementary motor area and basal ganglia, that plans sequences of movements. For example, having set the goal of where the serve is to land, the tennis player generates a sequence of movements that results in the ball moving as planned by the strategic process. The fourth process is a dynamic process, based in the spinal cord, that learns new spatial and temporal patterns of muscle activity.

The disparate representation principle proposes that these four processes use different forms of representation. Motor control entails several transformations of representation. The strategic process generates goals (i.e., what should be changed in the environment), and these goals are represented in allocentric space, a spatial frame in which objects are located relative to one another. The sequencing and perceptual-motor integration processes use an egocentric spatial frame, in which objects are located relative to some part of the body. The dynamic process represents movement in terms of patterns of muscle activity.

The dual mode principle proposes that there are two modes in which these four processes may operate when a task is performed. In the unconscious mode, shown in Figure 2A, a person generating a motor act (hereafter referred to as an actor) is aware only of setting the environmental goal; the other representations remain outside of awareness. For example, when reaching for a water glass an actor is aware of wanting to move the glass but unaware of the spatial target of the reaching movement; the spatial representations that drive movement are privileged to the motor system, and are not available to awareness (Goodale & Milner, 1992), as are the representations supporting the firing of particular muscles. When the conscious mode shown in Figure 2B, is engaged, the strategic process not only selects the environmental goal for the movement but also selects and sequences the spatial targets of the movement, thus replacing the sequencing and the perceptual-motor integration processes. The actor is aware of selecting the targets and sequencing them.

Most movements are made in the unconscious mode, because the sequencing and perceptual-motor integration processes usually do an adequate job of selecting and sequencing spatial targets. The conscious mode is usually invoked only when the actor believes that these transformations would fail. For example, a novice driver may engage the conscious mode when selecting how far to turn the steering wheel when turning. Nevertheless, either mode of control is available at any time. One can engage the conscious mode and actively select the target for even a simple movement, such as reaching for a glass of water.

The remainder of this section reviews findings supporting the psychological reality of these three principles in motor control.

## Neural Separability Principle

Motor behavior is often initiated when an actor has a goal that something in the environment be changed—that a magazine be moved from a table to a chair, for example—and this goal eventually results in overt movement. As Hollerbach (1982) has emphasized, the problem of motor control can thus be framed this way: What processes intervene between the goal and the muscle activation that results in movement? Behavioral and neural studies have provided a broad framework that is more or less agreed upon, and at the heart of this framework are four neurally separable processes, shown in Figure 1.

Strategic process: Selecting goals to change the environment. Motor behavior is initiated to satisfy a goal that something in the environment be changed. This goal is the product of processes outside of the motor system—for example, problemsolving and decision-making processes—and it is open to awareness. The actor can always verbally describe what change in the environment he or she is trying to bring about. This does not mean that each movement is consciously contemplated before it is initiated; rather, it means that the desired change in the environment is available to conscious processes for inspection or manipulation. The other representations supporting motor control are proposed to be closed to awareness, as shown in Figure 2A. The model proposes that the strategic process selects the goal of the movement.

The dorsolateral frontal cortex has been described as coding the goal of a movement, or coding movement planning in terms of behavioral significance (Jouandet & Gazzaniga, 1979; Luria, 1980; Milner & Petrides, 1984; Shallice, 1982). Luria described a number of patients with damage to the frontal lobe making errors of behavioral goals, for example, a woman sweeping a hot stove with a broom, or putting pieces of string into a pot instead of pasta. Such errors of setting incorrect environmental goals also occur in neurologically intact individuals, although less often (Norman, 1981).

Luria (1980) pointed out that patients with frontal lesions often repeat a goal inappropriately. This is the commonly observed phenomenon of perseveration. Frontal patients persev-

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Figure 1. Schematic diagram of the processes that contribute to motor control and motor skill learning and their locations in the brain. Heavy arrows show the primary processes that support learning, according to COBALT. Black circles show representations that are changed with learning. White circles show other representations necessary for skill learning.

erate because a mechanism that contributes to very-high-level planning of actions is faulty, so that once a plan is begun, it is difficult to change. Still other patients set fewer environmental goals as a result of their frontal lobe damage. This condition is called *abulia*, and it is characterized by a reduction in all activity. Such patients infrequently speak or move spontaneously, they answer questions briefly, and they are tolerant of the environments in which they are placed, often content simply to sit.

Single-cell recording studies in nonhuman primates support this interpretation of human lesions. They have indicated that dorsolateral frontal activity is related to whether an action is likely to elicit a reward, rather than to some aspect of the movement or to some physical characteristic of the stimulus; these neurons are therefore commonly referred to as coding behavioral significance (Barone & Joseph, 1989; Mann, Thau, & Schiller, 1988; Watanabe, 1990; Yamatani, Ono, Nishijo, & Takaku, 1990).

Imaging studies in humans have also implicated the dorsolateral frontal cortex in high-level planning of motor movements. Participants asked to choose freely where to move a joystick (compared with a condition in which they were to move the joystick to the same position on each trial) showed increased activity in the bilateral dorsolateral frontal cortex (Deiber et al., 1991; Playford et al., 1992; see also Frith, Friston, Liddle, & Frackowiak, 1991). Further, Parkinson's disease patients performing this task tended to choose the same direction on successive trials when they were instructed to choose randomly, and they showed less activation than control subjects in the bilateral dorsolateral frontal cortex (Playford et al., 1992).



Figure 2. A: schematic of the unconscious mode of executing skill. B: schematic of the conscious mode of executing skill. Shading indicates that the actor is not conscious of the contents of the representation.

Perceptual motor integration process: Selecting targets for movement. The posterior parietal cortex develops representations that serve as targets for end points of movement. A target is a spatial location to which an effector (e.g., the hand) moves. It is assumed that the end point of the movement guides control and that the entire trajectory of the movement is not computed (Bizzi, Hogan, Mussa-Ivaldi, & Giszter, 1992; Crossman & Goodeve, 1963/1983). As is consistent with the proposal that the posterior parietal cortex is involved in target selection, single-cell recording studies have shown that cells there respond vigorously during visually guided movements (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990), and ablation of the posterior parietal cortex causes inaccurate limb movements in both humans and nonhuman primates (for reviews, see Andersen, 1987; Hyvarinen, 1982). Although there is general agreement that the posterior parietal cortex supports these representations, there is controversy over their exact nature (see Stein, 1992, and accompanying commentary).

The posterior parietal cortex cannot by itself support visually guided movement; the premotor cortex appears to be critical for this function. A number of single-cell recording studies have indicated that the premotor cortex fires preferentially for visually guided movement (e.g., Godschalk, Lemon, Kuypers, & Van der Steen, 1985; Halsband, Matsuzaka, & Tanji, 1994; Mushiake, Inase, & Tanji, 1991). Functional imaging studies of visually guided reaching have also shown strong activity in the premotor cortex (Kawashima, Roland, & O'Sullivan, 1995). Lesion studies in humans and nonhuman primates, however, have shown that ablation of the premotor cortex does not have the profound impact on visually guided movements one might be led to expect (Freund, 1985; Passingham, 1985). As described below, premotor cortex lesions do have a profound impact on the learning of the relationship between perceptual cues and motor movements.

Sequencing: Assembling a sequence of targets. The posterior parietal cortex selects individual spatial targets, and the premotor cortex contributes to movements to these targets. The supplementary motor area appears to support sequencing of these targets as part of a cortico-basal-ganglionic-thalamo-cortical loop that goes from the supplementary motor area to the striatum, through the two major output stations of the basal ganglia (the substantia nigra and the globus pallidus) to the ventral thalamus, and then back to the supplementary motor area.

Damage to this neural circuit causes deficits in sequencing of motor behavior. Patients with damage to the striatum (the input station of the basal ganglia) due to Huntington's disease or Parkinson's disease have difficulty producing even simple motor sequences (Agostino, Berardelli, Formica, Accornero, & Manfredi, 1992; Agostino et al., 1994; Benecke, Rothwell, Dick, Day, & Marsden, 1987; Bradshaw et al., 1992; Harrington & Haaland, 1991; Thompson et al., 1988), as do patients with supplementary motor area infarcts (Dick, Benecke, Rothwell, Day, & Marsden, 1986; Gaymard, Pierrot-Deseilligny, & Rivaud, 1990; Halsband, Ito, Tanji, & Freund, 1993; Laplane, Talairach, Meininger, Bancaud, & Orgogozo, 1977). For example, in one paradigm used with all of these patient groups (Benecke et al., 1987; Dick et al., 1986; Thompson et al., 1988) participants were asked to move a lever, squeeze a bulb on the end of the lever, or move the lever and then squeeze the bulb, making the second movement the instant they complete the first. The patients performed the individual movements well but showed long delays between the movements when asked to do them sequentially.

This lesion evidence is supported by similar evidence from functional imaging studies. When participants are asked to execute a complex sequence of finger movements, there is activation of primary motor cortex as well as the supplementary motor area; when they are asked simply to imagine the sequence without executing it, the supplementary motor area is active but not the primary motor cortex (Rao et al., 1993; Roland, Larsen, Lassen, & Skinhoj, 1980). This finding suggests that the supplementary motor area plays a role in the planning of motor sequences. Single-cell recording studies in monkeys have shown that many supplementary motor area neurons fire exclusively in response to a particular movement only if it is made as part of a sequence (Tanji & Shima, 1994).

There has been some question, however, as to whether the basal ganglia and supplementary motor area contribute to sequencing or actually are important for making motor movements in the absence of visual guidance. These two principles are hard to separate, because making a multicomponent movement usually entails preparing movements at the end of the sequence before there is a cue in the environment to guide the movement. For a number of years, clinical reports have indicated that motor symptoms of Parkinson's disease patients are somewhat alleviated if they are given very salient visual targets (e.g., Forssberg, Johnels, & Steg, 1984), supporting the idea that the basal ganglia contribute to movement that is not guided by vision. But work that has more carefully manipulated the presence or absence of visual information has suggested that visual guidance is not so important to Parkinson's disease patients (e.g., Hocherman & Aharon-Peretz, 1994). Tanji, Mushiake, and Inase (1993) reported that some supplementary motor area neurons in monkeys are active during movements that are not visually guided, but these must be a sequence of movements; a simple movement made without visual guidance places no special demand on the supplementary motor area. In sum, it appears that the best interpretation of the function of the basal ganglia and supplementary motor area is that they contribute to motor sequencing, not to guiding movements in the absence of vision.

Dynamic: Innervating muscles. There are abundant singlecell recording data showing that the primary motor cortex codes movements in terms of space, not in terms of specific muscle commands (Georgopoulos, Kalaska, Caminiti, & Massey, 1982; Georgopoulos, Kettner, & Schwartz, 1988; Georgopoulos, Schwartz, & Kettner, 1986; Schwartz, 1992, 1993, 1995; but see also Scott & Kalaska, 1997). It is clear that eventually the neural code must be in terms of muscle commands, but neurons code movement spatially as late in the processing stream as the primary motor cortex. The primary motor cortex projects to interneurons in the spinal cord, which project to motoneurons, which innervate muscles. This sequence makes spinal interneurons likely candidates for the transformation from spatial to motor representation. It is true that other cortical areas (such as the supplementary motor area and the premotor cortex) send some direct projections to the spinal cord (Kunzle, 1978), but only a lesion restricted to the primary motor cortex (and not to other motor cortical areas) leads to paralysis; clearly the projection from the primary motor cortex to the spinal cord is crucial to motor control.

There is direct evidence from a series of experiments by Bizzi

and his colleagues that spinal interneurons are the site at which the spatial representation of movement is translated to a pattern of muscle activity (Bizzi et al., 1995; Bizzi, Mussa-Ivaldi, & Giszter, 1991; Giszter, Mussa-Ivaldi, & Bizzi, 1993; Mussa-Ivaldi & Giszter, 1994). They disconnected the spinal cord from the brain stem of a frog and microstimulated the spinal cord, causing the frog's muscles to generate forces, which they measured. On a number of trials the researchers stimulated the same spot in the spinal cord, varying the starting position of the leg. They found that the forces exerted by the muscles varied depending on the starting position of the leg and that these forces converged on an equilibrium point. Thus, stimulating a particular interneuron pool in the spinal cord resulted in muscle forces designed to place the leg at a particular end point in space. Direct stimulation of spinal motoneurons, on the other hand, led to force fields that did not converge on a particular point. Rather, stimulating motoneurons led to consistent force, no matter what the starting position, and, therefore, the end points of the movements varied. The cortical areas that innervate the spinal cord (primary motor cortex, supplementary motor cortex, premotor cortex) code movements spatially. (The rubrocerebellar system also projects to the spinal cord but appears to code force and velocity rather than spatial parameters of movement; see Keifer & Houk, 1994, for a review). Thus, interneurons seem to have the property of acting as networks that translate desired end points in space into patterns of muscle forces (through motoneurons) that move an effector to a spatial location.

These data are from amphibia and must be interpreted with caution in considerations of human movement. Still, they are consistent with evidence from human subjects with spinal cord compression, who often present with "numb, clumsy hands" syndrome (Chang, Liao, Cheung, Kong, & Chang, 1992). Their difficulty in making accurate movements may be in part the result of a lack of proprioception. This lack may not account for the problem entirely, however, because it is not completely alleviated by allowing patients to see their hands. In the present framework, pressure on the spinal cord may affect the translation from egocentric target to muscle activation, so that the effector is moved to the wrong location.

In summary, there is considerable evidence for localization of function in motor control. The prefrontal cortex is crucial for selecting a behavioral goal to be achieved by the movement. A target for the movement is generated in the posterior parietal cortex and communicated to the premotor cortex. If a sequence of targets is necessary for a movement to achieve the behavioral goal, the basal ganglia and supplementary motor area contribute to the sequencing of the targets. These spatial targets go to the spinal cord (via the primary motor cortex), where networks of spinal interneurons translate them into a pattern of signals, yielding a desired pattern of muscle activity.

# Disparate Representation Principle

Research indicates that there are three separate representations in motor control: allocentric space for goal selection in the strategic process, egocentric space for target selection in perceptual-motor integration and sequencing processes, and muscle innervation in the dynamic process.

Separation of allocentric and egocentric space. Much of

the planning of motor movements occurs in spatial coordinates, but the brain uses multiple spatial frames of reference. Researchers have made a broad distinction between two spatial representations: allocentric, in which objects' locations are coded relative to one another, and egocentric, in which objects' locations are coded relative to some part of the body (e.g., the hand, the head).

Much recent work has pointed to a fundamental distinction between spatial representations dedicated to conscious perception, which are allocentric, and spatial representations dedicated to movement, which are egocentric and not open to awareness. This division may begin as early as the retina (Livingstone & Hubel, 1988), but it becomes apparent in the anatomic connections from the primary and secondary visual cortex in the occipital lobe (Ungerleider & Mishkin, 1982), although recent evidence has pointed to greater communication between the two anatomic streams than was originally thought (Van Essen & Deyoe, 1995). One processing stream progresses ventrally into the temporal lobe and represents space allocentrically; the other processing stream progresses dorsally into the parietal lobe and represents space egocentrically.

A number of researchers have proposed that allocentric representations support perception and egocentric representations support motor behavior (Bridgeman, 1991; Jeannerod, 1994; Paillard, 1991; Rossetti, in press). It may seem odd to propose that different processes support perception and action-after all, introspection certainly indicates that when we reach for an object, it is the conscious percept that tells us where the object is located. But evidence from several paradigms tells us that that introspection is wrong; the percept is conscious, but a second, unconscious representation makes the accurate movement possible. Humans with lesions to the temporal cortex claim to have limited conscious visual perception of objects and are impaired in identifying even simple visual shapes. Nevertheless, they show normal motor behavior (e.g., positioning their hands correctly to make grasping movements, making visually guided eye movements). In contrast, patients with posterior parietal cortex lesions show normal visual recognition abilities (i.e., they can describe the shape of objects) and claim unimpaired perceptual awareness of object locations, and yet their reaching movements to the objects are grossly impaired (see Milner & Goodale, 1995, ch. 4, for a review). Single-cell recordings studies lend support to the lesion studies. At least some cells in the temporal cortex are object-centered; that is, they are insensitive to the view of an object-the cell responds equally well to a particular object whatever the angle from which it is seen, and thus codes space allocentrically (Perrett et al., 1991). Cells in the medial temporal lobe, and the hippocampus in particular, also code space allocentrically (Rolls, 1991). On the other hand, neurons in the posterior parietal cortex appear to code space egocentrically (e.g., Taira et al., 1990).

Environmental goal selection in allocentric space. In the simple control model shown in Figure 1, the environmental goal is coded in allocentric space and so the conscious, allocentric perceptual representation contributes to motor behavior only through the environmental goal. The spatial representations that are used to actually generate movements are egocentric.

There are several reasons to think that environmental goals are coded in allocentric space. First, environmental goals are, by definition, not specific to an effector; they describe a desired result of a movement in the environment. For example, an environmental goal may specify that a cup be moved from one location of a table to another, but it does not specify whether the cup should be moved with the hand, the elbow, or the chin. Egocentric space is defined relative to an effector, and so one must select an effector before one can set up an egocentric spatial representation. A second reason to propose that environmental goals are coded in allocentric space is that the locations of objects are likely coded that way already. Coding objects' location in egocentric space would not be helpful (except in planning movements) because such coding changes as the location of the body changes; as one moves, the location of objects coded egocentrically would constantly shift. Thus, the perception of objects as having stable locations relative to one another seems to dictate allocentric coding; and if object locations are coded in allocentric space, it seems sensible that changes in object location are planned in allocentric space.

COBALT proposes that the environmental goal not only uses an allocentric perceptual representation but also determines it. The allocentric location of objects in a scene may vary, because there cannot be a canonical allocentric spatial frame (Wraga, Creem & Proffitt, in press). A coordinate system must have a center-an anchor, so to speak. If the allocentric coordinate system is to be based in the environment, one or more landmarks in the environment must be selected to serve as this center-or as the boundaries of the coordinate frame. The theory as depicted in Figure 1 proposes that these landmarks are selected on the basis of the movement goal. For example, the allocentric representation of a book may be constructed in two different ways, depending on the goal. If the goal is to move the book on a desk, the book is coded as having a location in "desk space," with the boundaries of the desk providing the landmarks for the allocentric spatial coordinate system. If the environmental goal is to move a pen onto the book, the book itself provides the landmarks for an allocentric spatial location of the pen. Thus the allocentric spatial frame changes depending on the goal and the objects that are available to serve as landmarks. This is an assumption about which there is no evidence to date.

It is also possible to set the landmark for the allocentric spatial frame so that it is centered on a part of the body. Doing so can be useful in setting an environmental goal; for example, one might want to know how far an object is from an effector (e.g., whether it is in reach). In this case, one uses part of the body to set the allocentric spatial frame. This frame in a sense functions as an egocentric frame, because objects' locations are coded relative to part of the body, but it is not like an egocentric spatial frame in that the representation is used for perception and is not dedicated to the motor system. An allocentric representation when used in the conscious mode is considered isomorphic with an egocentric representation.

Target selection in egocentric space. Egocentric space depends on a coordinate system that is centered on some part of the body. There is considerable evidence that an egocentric representation is used by neurons in many of the cortical areas known to subserve motor control. Researchers have found evidence for spatial coordinate systems centered on the head (Bard, Fleury, & Paillard, 1990; Roll, Bard, & Paillard, 1986), shoulder (Caminiti, Johnson, & Urbano, 1990; Graziano, Yap, & Gross, 1994), and trunk (Yardley, 1990). For example, Caminiti et al. recorded from individual cells in the primary motor cortex of

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monkeys as they made reaching movements. Each neuron fired maximally when a monkey reached in a particular direction. By changing the orientation of the animal it was possible to determine the spatial reference frame these neurons used, and the results were consistent with a spatial frame centered on the shoulder. From this and other work, it is now clear that coding in the primary and secondary motor cortices (including the premotor cortex, and dorsal and ventral aspects of the secondary motor area) is in terms of egocentric space (Graziano et al., 1994), as shown in Figure 1.

*Muscle innervation.* The very fact that movement occurs through muscle activity indicates that the central nervous system must, at some point, code movements as a pattern of muscle activity. As described above, spinal motoneurons clearly use a representation of muscle forces.

In summary, COBALT embodies the disparate representation principle by proposing that the strategic process uses an allocentric spatial representation, the perceptual-motor integration and sequencing processes employ an egocentric spatial representation, and the dynamic process uses a representation of motor activity.

# **Dual Mode Principle**

The dual mode principle proposes that all voluntary actions are initiated by a conscious environmental goal. The subsequent transformations-perceptual-motor integration, sequencing, and dynamic-generate representations for the movement, and they do so outside of awareness. If an act is executed in the unconscious mode, movement results. If the act is executed in the conscious mode, the strategic process that selects the environmental goal also generates the targets for movement and sequences them, replacing the perceptual-motor integration and sequencing processes. These processes do not generate representations if the conscious mode is engaged. It appears to be possible for subjects to consciously select specific muscle groups to contract, that is, to replace the dynamic process (e.g., Cohen, Brasil-Neto, Pascual-Leone, & Hallett, 1993), but COBALT does not attempt to account for this ability, which seems to be invoked rarely outside of the laboratory.

COBALT proposes that using the conscious mode has three consequences: First, the environmental goal is coded not in allocentric space, but in egocentric space. Second, the actor is aware of the sequence of egocentric targets. Third, making the movement is more demanding of attention than it would be were it executed in the unconscious mode.

The strategic process can use only allocentric representations. As described above, there is not a canonical allocentric spatial frame. The theory proposes that the strategic process can set the allocentric spatial frame to correspond to egocentric space. As noted earlier, this process can be useful in setting environmental goals—for example, when trying to determine whether an object is close enough to be reached. When the conscious mode is engaged, the theory assumes that the locations of objects are coded relative to effectors, in an allocentric representation that functions as an egocentric representation.

The actor is proposed to be aware of the sequence of spatial targets when the conscious mode is engaged because the product of the strategic process is always open to awareness. The strategic process is proposed to be demanding of attention, whereas the perceptual-motor integration, sequencing, and dynamic processes are not. Hence, responding in the conscious mode is more demanding of attention than responding in the unconscious mode.

When is the conscious mode engaged? The accuracy of the transformations generated in the unconscious mode is proportional to the actor's experience with similar tasks, because the experience level dictates the extent to which these transformations have been tuned to the task. Typically, an actor uses the conscious mode when performing an unfamiliar task (e.g., learning to drive) because use of the unconscious mode would lead to inaccurate transformations. As the actor gains experience with the task, the transformations are tuned to it, and the unconscious mode eventually generates sufficiently accurate transformations that the conscious mode need not be invoked.

The idea that a new motor task is attention-demanding, and that the attention demands decrease with practice, goes back at least to James (1890). There is a wealth of evidence supporting this idea, generally referred to as the *development of automaticity* (see Logan, 1985, for a review). There has been less focus on the idea proposed in the dual mode principle: that even a well-practiced skill, such as reaching, can be executed in the conscious, attention-demanding manner of a novel skill. It is commonly appreciated that automatic skills may become attention-demanding if a task becomes difficult. For example, even an experienced driver may turn off the radio in order to focus attention on driving when a road is icy. Introspection indicates that it is possible to engage the conscious mode at any time, not just when a task becomes difficult. One can reach for a glass, for example, and attend to the spatial target of the movement.

Recent neuroimaging evidence indicates that attending to an automatic process in this way truly does engage different brain processes. Jueptner et al. (1997) asked participants to learn sequences of eight finger movements. The prefrontal cortex was activated during learning, but not during automatic performance once the sequence was well-learned. The prefrontal cortex was again activated, however, when participants were asked to attend to their performance.

## Motor Skill Learning in COBALT

The preceding section described a basic architecture of motor control based on three principles. This section shows how this architecture can support motor skill learning.

Two mechanisms support motor skill learning in COBALT. First, the perceptual-motor integration, sequencing, and dynamic processes may become more efficient for a particular task. Each time a task is performed, each of these three processes is tuned to the task, making the transformation it performs more accurate. The second mechanism of learning is through the strategic process, which is not tuned as the other processes are. Rather, it may contribute to improved performance either by selecting more effective environmental goals or by selecting and sequencing more effective targets for movement when the conscious mode is invoked.

# Learning Through the Tuning of Individual Processes

One mechanism of learning is the tuning of transformations so that they become more efficient: The perceptual-motor inte-

gration, sequencing, and dynamic processes may be tuned. This tuning process is proposed to operate similarly to the tuning of a parallel-distributed processing network employing the delta rule (see Rumelhart & McClelland, 1986, for examples and detailed discussion). The following assumptions are made about learning via this tuning process: First, learning occurs if and only if a movement is executed. Learning is based on the movement that is actually produced, so movement must occur for learning to occur. The perceptual-motor integration and sequencing processes are tuned if they produce the representations for the movement-or if the strategic process does, through the conscious mode. Thus, the conscious mode "turns off" the unconscious mode in terms of performance, but not in terms of learning. Second, feedback regarding accuracy is necessary for learning to occur. This feedback may simply be the actor's evaluation of the success of the movement, or it may be some augmented form of feedback from the environment. Third, although the process is changed (i.e., tuned) every time a movement is executed, each of these changes is small. Fourth, just as it was assumed in the description of the dual mode principle that the perceptual-motor integration, sequencing, and dynamic processes operate outside of awareness, it is assumed that the tuning of these processes occurs outside of awareness as well.

In the remainder of this section, the types of tasks that are supported by the tuning of each process are described.

Perceptual-motor integration learning. Typically, the selection of an egocentric spatial target for movement is easy, because the target for a movement is usually the same as the location of its object; if one wishes to grasp a pencil, the end point for the movement is the pencil. That is not to say that the selection of the target is a trivial computational problem, but target selection is so highly practiced that learning is unnecessary. For example, when asked to perform a reaching task with a spatially compatible mapping, participants approach asymptote quickly, in as few as 10 trials (Kawashima et al., 1995).

There are two ways that target selection can become difficult. The first is that the relationship between vision and proprioception can be changed. For example, it can be manipulated in the laboratory by asking participants to wear wedge-prism spectacles, which displace the visual world 30° to the right. When asked to point to locations in space, participants initially make large errors, but they show rapid learning. The relationship between vision and proprioception also changes in less artificial situations outside of the laboratory, but on a much longer time scale; proprioception changes as the body grows, slowly influencing egocentric spatial representations. Therefore, there must be some adjustment of the transformation between behavioral goals (which are represented in allocentric space) and spatial targets (which are represented in egocentric space).

Target selection can also become difficult when the correct location of an egocentric target differs from the location of the object. If one wants to touch a peg with one's finger, the location of the peg is identical to the egocentric target for the finger to move to. But if one wants to hit a peg with a hammer, the egocentric target to which one should move one's fist is certainly not identical to the location of the peg. Using a hammer poses no great challenge for adults because they are practiced in manipulating rigid objects. Other, less practiced tasks—for example, using a computer mouse—are difficult even for adultsand indeed, the effective use of a mouse requires learning (Willingham & Koroshetz, 1993).

Sequencing learning. The sequencing process is tuned every time it is engaged. Therefore, sequence learning is proposed to take place in any task that requires the actor to select the same sequence of egocentric spatial targets repeatedly. For example, when learning to serve a tennis ball, one makes the same movements again and again. Indeed, the goal is to stereotype the stroke; one would like the movements to be identical every time it is executed. In the laboratory, the pursuit rotor task, in which a participant uses a hand-held stylus to track a target moving in a circle (see Table 2), similarly has a strong sequencing component. Because of the repetitive movement of the target, the same sequence of egocentric targets is called for again and again, and that is a necessary and sufficient condition for sequence learning to occur. By virtue of setting up the same sequence of targets repeatedly, the sequencing process becomes tuned to generating that particular sequence of targets.

Dynamic learning. The final transformation for control occurs when targets in egocentric space are transformed into a spatial and temporal pattern of muscle contraction that moves effectors to these targets. This transformation is highly practiced—it occurs every time a nonreflexive movement is madeand the relationship between egocentric spatial targets and the correct pattern of muscle contraction rarely changes. Changes in the body such as disfigurement or growth require learning to take place. Learning may also be observed when strong demands are consistently placed on an effector for more spatially accurate movements. For example, the fingers of the nonpreferred hand or the toes are seldom called upon for a task requiring dexterity; but they can become dexterous given sufficient practice (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995), and COBALT posits that this improvement is the result of learning in the transformation between egocentric spatial targets and the pattern of muscle contraction.

COBALT proposes that dynamic learning contributes to motor skill learning under all circumstances, not only when an unusual effector is used or in association with growth or disfigurement. The transformation between egocentric targets and muscle commands is always being tuned by experience. It may take a very long time (on the order of hundreds of trials) to affect performance if the experience a task provides is not very different from the experience that most tasks provide. Because the relationship between egocentric space and the muscle plant changes very little across tasks, the transformation is more or less ready to go when an actor begins the task. With enough practice in one context, however, the dynamic process is tuned so that it is somewhat specialized for the training task. Learning in this process is slow to affect performance because a lifetime of experience makes the egocentric space-muscle plant transformation quite efficient to start with.

## Learning Through the Strategic Process

The strategic process can contribute to learning in two ways: It can select more effective high-level goals, and it can select and sequence more effective spatial targets for movement, via the conscious mode.

How does the strategic process come up with more effective high-level goals, or with a new sequence of spatial targets for

## Table 2

Description of Tasks Commonly Used in Motor Skill Learning Experiments

Task	Description	Processes engaged in learning
Serial response time	Participants complete four-choice response time task in which, unbeknownst to them, the stimuli appear in a repeating sequence.	Comparison of response times when the stimuli appear in the sequence to when they appear randomly is a measure of <i>sequence</i> learning. Participants may engage the conscious mode if they become aware of and explicitly memorize the sequence, in which case <i>strategic</i> processes also contribute.
Incompatible serial response time	Participants complete a four-choice response time task that uses an incompatible stimulus-response mapping.	Stimuli are not sequenced, so learning is primarily perceptual-motor integration learning.
Pursuit rotor	Participants try to keep the tip of a hand-held stylus on a target moving in a circle.	This is primarily a <i>sequence</i> learning task, because of the repetitive movement of the target.
Prism-spectacles adaptation	Participants point to visual targets while wearing prisms that make visual and proprioceptive feedback disagree.	The two feedback types become recalibrated with practice by means of <i>perceptual-motor integration</i> learning. Participants may engage the conscious mode if they gain explicit knowledge of the transformation, in which case <i>strategic</i> processes also contribute.
Prism-spectacles aftereffects	After some experience wearing prism spectacles, participants remove the spectacles and are asked to point directly in front of their noses with eyes closed.	This task measures recalibration of vision and proprioception without any contribution from strategic processes in the conscious mode; the spectacles are removed, so the participant has no reason to engage those strategic processes. Thus it is a perceptual-motor integration task.
Mirror tracing	Participants are asked to trace a figure, but they can see the figure, pen, and hand only in a mirror; an occluding screen prevents their seeing them directly.	This is another instance of learning a new stimulus- response mapping and therefore of <i>perceptual-motor</i> <i>integration</i> learning. Participants tend not to gain conscious knowledge of the mirror transformation.
Explicit sequence learning	Participants are given a sequence to learn (either of finger-thumb opposition movements or of key presses), to explicitly remember, and then to perform.	This task taps the <i>strategic</i> process via the conscious mode. Simultaneously, the <i>sequencing</i> process is engaged.
Learning to use a computer mouse or joystick	Participants are asked to track or trace a stimulus on a computer screen by using a mouse or joystick.	Participants see a direction in which they want the cursor to move and must learn the appropriate motor response to make it move in that direction. This task is an instance of learning a new stimulus- response mapping and therefore of <i>perceptual-motor</i> <i>integration</i> learning.

movement? The strategic process has access to explicit, conscious knowledge, so a coach's instruction, for example, is mediated through the strategic process. An actor may also obtain knowledge about effective environmental goals to set, or about effective sequences of spatial targets, by observing other actors performing a task.

In addition to observation and instruction, actors generate their own hypotheses about new environmental goals to set, and make decisions about which sequence of spatial targets to use, in the conscious mode. COBALT proposes that the processes underlying these hypotheses and decisions are akin to highlevel problem-solving processes. At present, the theory does not provide an account of how they are generated. It does, however, account for the way they are used.

Strategic learning through environmental goal selection. The improved selection of high-level goals is easy to appreciate and corresponds to the common use of the word strategy. A tennis player may notice (or be told) that his or her opponent's backhand is weak, and so the player then frequently hits to the opponent's backhand as an environmental goal. Another example is a driver's learning that it is more effective to pump the brakes when stopping on a slippery road. The use of such strategies is seldom obvious in laboratory tasks. Laboratory tasks are usually quite simple—for example, pursuit-tracking or button-pressing—and so, although participants may adopt different

strategies, there is not a simple way to measure or quantify them.

Strategic learning through the conscious mode. The strategic process can also contribute to improved performance through the conscious mode by doing some of the planning that is usually performed by unconscious processes, namely selecting targets in egocentric space and sequencing them, as shown in Figure 2B.

Conscious selection of the egocentric target can improve performance in some motor skill learning tasks, for example, reaching while wearing prism spectacles (Redding & Wallace, 1996). In the typical experiment (see Table 2) the mismatch between vision and proprioception leads participants to point inaccurately. Participants can greatly improve performance in this task by consciously selecting a target to point to that looks wrong, that is, a target that appears 30° to the left of the actual target. According to the model, the perceptual-motor integration process selects an egocentric target that does not account for the spectacles, and so participants initially point to the wrong location. Participants who then consciously point to a target that looks wrong are engaging the strategic process, which selects a target based on the conscious knowledge that the spectacles require a correction in pointing. The strategic process thus replaces the perceptual-motor integration process.

In other motor skill learning tasks, selecting individual targets

is not difficult, but sequencing them rapidly is. For example, in the serial response time task, participants are asked to perform a four-choice response time task with a compatible mapping (see Table 2). The stimuli appear in a repeating sequence, usually 12 units long. If participants are not told about the repeating sequence, they often do not notice it, because nothing marks the beginning or end of the sequence; nonetheless, response times decrease with training on the sequence and increase if the stimuli begin to appear randomly. Thus, it is apparent from their performance that participants learn the sequence (Nissen & Bullemer, 1987; Willingham, Nissen, & Bullemer, 1989). According to COBALT, such learning is handled by the unconscious sequencing process. Participants may also learn the sequence consciously; such learning further improves performance. Participants who are first asked to memorize the sequence show a substantial benefit in response time-in fact a greater benefit than that shown by those who remain unaware of the sequence (Curran & Keele, 1993). According to COBALT, such learning is a result of the strategic process sequencing the targets for movement.

The proposal of the conscious mode's operation may seem surprising, because being able to describe how to execute a task (i.e., being conscious of the procedure) clearly does not mean one can actually do it. For example, one may tell a beginning tennis player that to hit an American twist tennis serve the ball should be tossed behind the head, the back arched, and the ball hit upward and away from the body. The player now has some strategic knowledge about how to hit the serve; does the theory predict that the serve will immediately be successfully executed? Not exactly. The theory predicts that the beginning player will be more successful with strategic knowledge than without it. If two beginning players have the same environmental goal in mind (hitting an American twist serve), the player with strategic knowledge will be much more likely successfully to execute the serve first, according to the theory, because he or she will use the strategic process to approximate the correct form. Further, the theory holds that the usefulness of strategic knowledge depends on its precision regarding spatial targets. The strategic knowledge offered above does not give specific spatial targets, whereas in the serial response time task the spatial targets are defined by the task, and so strategic knowledge can be quite precise.

# The Principle of Neural Separability and Motor Skill Learning

In this section, the predictions allowed by the neural separability principle are described, as well as data bearing on those predictions.

The neural separability principle allows two strong predictions. First, dissociations of motor skill learning should be observed. At first glance it appears that some patients are impaired in learning all new motor skills, and other patients can learn any motor skill. For example, it has been reported that the basal ganglia (Salmon & Butters, 1995) and the cerebellum (Sanes, Dimitrov, & Hallett, 1990) are important to motor skill learning, implying that patients with basal ganglia or cerebellar damage should be impaired in learning motor skills. The neural separability principle posits, however, that if a patient suffers an insult to just one of the brain regions that supports motor skill learning, only one motor skill learning process should be affected; the patient should be able to learn any task that does not require a contribution from that process. Dissociations in motor skill learning should be observed because the processes operate independently. The processes operate independently because they are simply transformations. If the input to a process is faulty, the output of the process may be faulty, but the transformation may still be learned. For example, an actor may select a poor environmental goal (e.g., trying to hit the tennis ball into the net) but the perceptual-motor transformation (where to move the hand so that the head of the racquet hits the ball) can still be learned. In positing that dissociations of skill learning should be observed, COBALT is in stark contrast to other accounts of the neural basis of motor skill learning, which argue that an individual structure may contribute to the learning of motor skills of all different types (Heindel, Salmon, Shults, Walicke, & Butters, 1989; Salmon & Butters, 1995; Sanes et al., 1990).

The second prediction is that one should be able to predict which brain structures will show activity during functional imaging while motor skill learning occurs. A quick glance at the studies using functional imaging techniques shows that a large number of brain structures and cortical areas have been implicated in motor skill acquisition, as shown in Table 1. It is not at all clear what each does, however, or even whether each contributes directly to motor skill acquisition. COBALT posits that a specific brain structure should be active to the extent that the task requires the motor skill learning process that that brain structure supports. The conditions under which the different motor skill learning processes are engaged were discussed above and are summarized in Table 3.

The remainder of this section evaluates the predictions summarized in Table 3. It is organized according to the processes in COBALT and is followed by a section comparing the predictions of COBALT with predictions of other theories.

# Strategic Tasks

COBALT posits that the dorsolateral frontal cortex supports a process by which an actor may discover a new, more effective way to perform a task, that is, a new environmental goal to set. Laboratory tasks that have been used in the past make it difficult to assess this sort of improvement. Most are tracking or buttonpressing tasks, and there is not a straightforward way to assess whether participants adopt different strategies in these tasks, that is, set different environmental goals.

There is considerable evidence, however, from nonmotoric tasks, that strategy formation is difficult for human patients with frontal lobe damage (Duncan, 1986; Jouandet & Gazzaniga, 1979; Milner & Petrides, 1984). Frontal patients have particular problems with divergent thinking (Milner, 1964; Zangwill, 1966); that is, they have difficulty generating many possible solutions to a problem, and they also have trouble in shifting strategies once they have begun a task, even if it is plain that the initial strategy is no longer effective (Drewe, 1974; Milner, 1964). These abilities are exactly what the strategic process makes possible, and it is therefore likely that the difficulties that frontal patients show in the nonmotoric domain should carry over to motor skills. Other researchers have had little to say about the consequences of frontal lobe damage on motor skill

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Table 3			
Summary	of Processes	in	COBALT

Process	Anatomic location	When engaged	Example		
Strategic	Dorsolateral frontal cortex	Possibly, tasks for which more than one environmental goal is selected	Tennis player selecting to opponent's backhand		
Sequencing	Supplementary motor area, basal ganglia	Tasks that require the same sequence of egocentric targets to be selected repetitively	Tennis serve; pursuit rotor task		
Perceptual-motor integration	Posterior parietal cortex, premotor cortex	Mismatch between vision and proprioception or mismatch between the site of action in allocentric space and the egocentric target	Adjusting to prism spectacles; hitting a nail with a hammer		
Dynamic	Pools of spinal interneurons	Mismatch between egocentric target and muscle movement	Fine motor use with an effector seldom used for this purpose (e.g., nonpreferred hand)		

acquisition, but they have often speculated that the learning of sequences is compromised.

The other function of the strategic process is its role in the conscious mode of selecting egocentric targets and sequencing them. The important characteristic of this function is that participants become aware of the necessary sequence of movements (in which case it replaces the unconscious sequence learning process) or of the transformation necessary to select accurate egocentric targets (in which case it replaces perceptual-motor integration learning). Two commonly used laboratory tasks offer the opportunity for this sort of strategic learning: the prism adaptation task and the serial response time task.

Wedge prism spectacles shift the visual world (usually 30°). Adjusting movements to prism spectacles combines two processes: It is a perceptual-motor integration task-a new mapping between vision and proprioception must be learned-and it can also be a strategic task-the participant may deduce the nature of the transformation the spectacles introduce and use that conscious representation to select an egocentric target to point to. Thus, training with prism spectacles measures the combined learning of these two processes. It is possible to look at perceptual-motor integration learning in isolation, however. After training, a participant can be asked to remove the spectacles, close his or her eyes, and point directly in front of his or her nose. Pointing directly in front of the nose provides a measure of the extent to which proprioception has been adjusted to the altered visual feedback of the spectacles; participants usually point 5° to 10° in the direction opposite to that of the prism; this is called a prism aftereffect. Because the spectacles are removed, the participants should not apply any conscious strategies in this test (assuming they do not know that the prism spectacles have affected proprioception). The measure of the aftereffect is, then, a measure of perceptual-motor integration. Thus, COBALT posits that patients with impairment to the strategic process should be impaired when pointing while wearing prism spectacles, but not on the aftereffects test, because that test is a measure of perceptual-motor integration.

Patients with lesions to the frontal lobe are indeed impaired in learning to point while wearing prism spectacles (Canavan et al., 1990). COBALT predicts they should show normal adaptation aftereffects; they have not yet been so tested.

Huntington's disease patients should be similarly impaired because they usually are at least mildly demented and show deficits on tests sensitive to frontal lobe function, probably as a result of deafferentation of the frontal lobe due to striatal degeneration. Huntington's disease patients are significantly impaired in pointing when wearing prisms. Early Huntington's disease patients show a normal adaptation aftereffect, as predicted, although moderate Huntington's disease patients are marginally impaired (Paulsen, Butters, Salmon, Heindel, & Swenson, 1993). Alzheimer's disease patients also show dementia, so COBALT predicts they should be impaired while pointing with prisms. In one report, patients were thus impaired (Weiner, Hallett, & Funkenstein, 1983), whereas in another they were not (Paulsen et al., 1993); but both studies reported that patients showed normal aftereffects.

Parkinson's disease patients vary in the extent to which they show frontal signs. As in Huntington's disease patients, the frontal lobe may be in part deafferented as a result of striatal abnormalities caused by dopamine depletion, and later in the disease there is degeneration of the ventral tegmental area, the primary source of dopamine to the frontal lobe (Uhl, Hedreen, & Price, 1985). Thus, the extent to which Parkinson's disease patients show neurological signs associated with frontal lobe damage varies (Growdon & Corkin, 1986; Taylor, Saint-Cyr, & Lang, 1986); there are therefore individual differences in Parkinson's disease patients in the extent to which they fail on motor skill learning tasks that demand strategic processing; these failure rates should be predictable, however, by the extent of their dementia. Weiner et al. (1983) reported a marginal (but not statistically reliable) impairment in Parkinson's disease patients in pointing with prism spectacles and normal aftereffect. Canavan et al. (1990) reported that Parkinson's disease patients were impaired during training; these patients were not tested for aftereffects.

Strategic processes may also be brought to bear in the serial response time task. Participants are not told that the stimuli in this task appear in a repeating sequence, but usually some notice the sequence and are able to use this information to greatly improve response times (Willingham et al., 1989). COBALT posits that if the strategic process is impaired, participants should be less likely to notice the repeating sequence. Indeed, studies have shown that Alzheimer's disease patients exhibit normal unconscious sequence learning (Willingham, Peterson, Manning, & Brashear, 1997); or most exhibit normal learning, with a minority showing poor learning (Ferraro, Balota, & Connor, 1993; Knopman & Nissen, 1987); but virtually none become aware of the sequence. It should be noted, however, that awareness of the sequence is difficult to assess in Alzheimer's disease patients because of the explicit memory deficits; nonde-

mented amnesic patients also fail to become aware of the sequence (Nissen, Willingham, & Hartman, 1989; Reber & Squire, 1994) presumably because of their inability to remember it explicitly.

A number of functional imaging studies have examined strategic processes in motor skills, typically in conjunction with sequencing tasks. These studies sharply illustrate the distinction between the conscious and unconscious modes the model proposes; the prefrontal cortex is activated in situations when the conscious mode is used. In the explicit sequence learning task, participants are asked to tap their thumbs against opposing fingers in a particular sequence (see Table 2). They must first memorize the sequence, so the task clearly uses the conscious mode, and activity is observed in the prefrontal cortex as well as the premotor cortex and supplementary motor area (Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994; Schlaug, Knorr, & Seitz, 1994; Seitz & Roland, 1992; Seitz, Roland, Bohm, Greitz, & Stone-Elander, 1990). Seitz et al. (1990) reported that frontal activation decreases with practice, and this decrease occurs when participants report they no longer need to count the finger taps internally.

This last finding is similar to those reported with the serial response time task. In that task, participants are initially unaware of the sequence, but they may take note of and memorize it as training progresses. In the serial response time paradigm, experimenters take careful measures of sequence awareness during the experiment. Unconscious sequence learning in the serial response time task is associated with activity in the supplementary motor area, premotor cortex, and striatum, but when a participant becomes aware of the sequence, there is also activity in the dorsolateral frontal cortex and parietal cortex (Doyon, Owen, Petrides, Sziklas, & Evans, 1996; Grafton, Hazeltine, & Ivry, 1995; Rauch et al., 1995). These findings are also consistent with those of Pascual-Leone, Grafman, and Hallett (1994), who reported that cortical motor maps in the primary motor cortex increase in size with training on serial response time, but then abruptly return to baseline when a participant becomes aware of the sequence.

According to COBALT, once a participant is aware of the sequence, he or she uses the conscious mode, and the knowledge in cortical motor areas is rendered irrelevant. In all of these studies there was little overlap in areas of activation when the participants were conscious of the sequence versus when they were unconscious. The theory predicts that the sequencing process is tuned even when the conscious mode generates representations for movement; why, then, is there not striatal activity in the conscious participants? Striatal activity may not be observed because once the conscious mode is engaged the striatum no longer sequences movements. Although the striatum is tuned, that state may not represent sufficient neural activity to generate statistically reliable differences among imaging scans.

## Perceptual-Motor Integration Tasks

Tasks that have a strong perceptual-motor integration component are those that change the relationship between vision and proprioception (as prism spectacles do) or those for which the site of action of an object is not the same as the object's location (as in tool use). Three task paradigms that require perceptualmotor integration have frequently been used: tasks with arbitrary or incompatible mappings, tracking tasks, and prism spectacles tasks. For all three, COBALT posits that damage to the posterior parietal cortex or premotor cortex should lead to impaired learning, because those sites support the perceptual-motor integration process. Learning should be intact in the face of damage to other brain structures.

A great deal of work in nonhuman primates has examined the neural basis of conditional motor learning, that is, the learning of an arbitrary perceptual-motor association (e.g., a red light signalling that a handle should be twisted, and a green light that it should be pulled). Work in both monkeys (Halsband & Passingham, 1982; Passingham, 1987; Petrides, 1982) and humans (Halsband & Freund, 1990; Petrides, 1985) has shown that damage to the posterior parietal cortex or premotor cortex (but not other cortical areas) leads to profound difficulty in learning these perceptual-motor associations. Other associations, such as a reward relationship between two visual stimuli, can still be learned. Thus, COBALT can account for this pattern of results.

A variety of paradigms using incompatible stimulus-response mappings have been administered to humans, most often to patients with basal ganglia abnormalities as a result of Huntington's disease, which is marked by striatal degeneration (both caudate and putamen), or Parkinson's disease, which causes cell death in the substantia nigra, zona compacta, the primary source of dopamine to the striatum. Huntington's disease and Parkinson's disease patients show normal rates of speed improvement on a button-pushing task with an incompatible mapping (see Table 2; Robertson & Flowers, 1990; Willingham & Koroshetz, 1993), and they learn to trace a pattern viewed in a mirror normally (see Table 2: Agostino, Sanes, & Hallett, 1996; Frith, Bloxham, & Carpenter, 1986; Gabrieli, Stebbins, Singh, Willingham, & Goetz, 1997). Huntington's disease patients also learn how to use a computer mouse or joystick normally (Willingham & Koroshetz, 1993; Willingham, Koroshetz, & Peterson, 1996). These results are consistent with COBALT, because although these patients have severe motor disabilities, the parietal lobe and premotor cortex are relatively intact in the early stages of the diseases, and so perceptual-motor integration learning is normal. These results are also important because they show that the deficits exhibited by striatal patients on sequencing tasks are not simply due to a widespread dementia; although striatal patients do show a number of cognitive deficits (Brandt & Butters, 1986; Mayeux & Stern, 1983), their impairment in sequencing tasks cannot simply be attributed to a broad cognitive deficit, because they learn other motor skills normally.

Patients with Alzheimer's disease have widespread cortical degeneration and particular problems with explicit memory (Arnold, Hyman, Flory, Damasio, & Van Hoesen, 1991; Nebes, 1992). Although parietal degeneration is associated with Alzheimer's disease, spatial problems are not a consistent feature of the disease (Henderson, Mack, & Williams, 1989); COBALT posits that Alzheimer's disease patients should learn new perceptual-motor integration skills normally. Indeed, they can learn a mirror tracing task (Gabrieli, Corkin, Mickel, & Growdon, 1993), and they learn normally the relationship between joystick and cursor movement (Willingham et al., 1997).

As described above, adjusting to prism spectacles combines two processes. It is a perceptual-motor integration task—a new mapping between vision and proprioception must be learnedand it can also be a strategic task—the participant may deduce the nature of the transformation the spectacles introduce and use that conscious representation to select an egocentric target to point to. The measure of the aftereffect is a measure of perceptual-motor integration. As COBALT posits, the normal aftereffect is observed in Alzheimer's disease (Paulsen et al., 1993; Weiner et al., 1983) and early Huntington's disease, although moderate Huntington's disease patients show a trend toward a deficit (Paulsen et al., 1993). Recent neuroimaging work supports the prediction that the posterior parietal cortex is the critical site of learning. Clower et al. (1996) reported that a very restricted site of activation in the posterior parietal cortex is associated with adaptation.

## Sequencing Tasks

COBALT holds that the basal ganglia and supplementary motor area support the sequencing process, and therefore that patients with basal ganglia abnormalities because of Huntington's disease or Parkinson's disease should be impaired on sequencing tasks. One such task is the pursuit rotor task, in which participants are asked to keep the tip of a stylus in contact with a small disk that moves repetitively in a circle. This is a sequencing task because the same sequence of spatial targets is required on each trial (see Table 2). Huntington's disease patients are consistently impaired on this task (Gabrieli et al., 1997; Heindel, Butters, & Salmon, 1988; Heindel et al., 1989; Willingham et al., 1996). Harrington, Haaland, Yeo, and Marder (1990) found that early Parkinson's disease patients learned the pursuit rotor task, whereas patients with moderate disease did not; almost all of these patients were taking dopamine-replacement medication at the time of testing, however. Bondi and Kaszniak (1991) reported normal learning in their group of Parkinson's disease patients, but they used a computer version of the task, and participants used the mouse to respond. It is possible that these participants primarily learned to use the mouse (a perceptual-motor integration skill; see Table 2) but did not really learn the sequential aspect of the task.

Willingham et al. (1996) directly tested the hypothesis that the pursuit rotor deficit was the result of difficulty with sequencing. They administered a computer analog of the pursuit rotor task (Willingham, Hollier, & Joseph, 1995) in which patients tried to track a moving target by manipulating a crosshair cursor with a joystick. When the target moved in a repeating sequence, Huntington's disease patients' learning was impaired, but when it moved randomly, Huntington's disease patients learned normally. The authors argued that when the target moved randomly participants could learn the relationship between joystick movement and cursor movement, and when it moved in a repeating sequence, neurologically intact participants could also learn the repeating sequence of movements. Huntington's disease patients could not learn the sequencing aspect of the task and so were impaired when the target moved in a repeating pattern.

Huntington's disease and Parkinson's disease patients have also been tested on the serial response time task, the four-choice response time task with a repeating sequence of stimuli. The advantage of the serial response time task is that one can look at sequence learning in relative isolation by comparing responses when the stimuli are sequenced and when they appear randomly. Huntington's disease patients show poor learning of the sequence (Knopman & Nissen, 1991; Willingham & Koroshetz, 1993); Parkinson's disease patients are also so impaired (Ferraro et al., 1993; Jackson, Jackson, Harrison, Henderson, & Kennard, 1995; but see also Pascual-Leone et al., 1993).

COBALT posits that patients with basal ganglia or supplementary motor area disorders should be impaired in sequencing, but that the sequencing process can operate independently in the face of damage to other structures. Therefore, Alzheimer's disease patients should learn the serial response time task normally, and they do (Ferraro et al., 1993; Knopman, 1991; Knopman & Nissen, 1987), as do patients with frontal lobe damage (Marks & Cermak, 1996). Alzheimer's disease patients also learn the rotary pursuit task normally (Bondi & Kaszniak, 1991; Deweer et al., 1994; Dick, Nielson, Beth, Shankle, & Cotman, 1995; Eslinger & Damasio, 1986; Heindel et al., 1989).

Functional imaging studies, like the lesion studies, lead to the conclusion that the basal ganglia and supplementary motor area are crucial for sequencing tasks. Participants performing rotary pursuit show learning-associated activation in a number of cortical and subcortical structures, but the strongest activation is in the supplementary motor area (Grafton et al., 1992; Grafton, Woods, & Tyszka, 1994). In one study (Rauch et al., 1997), the learning scores in the serial response time task were correlated with putamen activity; in another (Granholm, Bartzokis, Asarnow, & Marder, 1993), the learning scores of schizophrenic patients on the pursuit rotor task were correlated with a measure of their caudate activity in functional Magnetic Resonance Imaging (fMRI). Learning in the serial response time task in normal participants is also associated with activity in the supplementary motor area and striatum (Doyon et al., 1996; Grafton, Hazeltine, & Ivry, 1995).

# Temporal Course of Brain Activation

Functional imaging techniques allow the assessment of not only which brain areas are active during learning of a motor skill, but also of the changes in brain activity during the course of learning. Many studies have evaluated these changes; they are summarized in Table 4. Note that this table reflects the changes in activity from early training to late training; a decrease in activity may mean that there is a great deal of activity early in training, but less activity late in training—it does not mean that there is a depression of neural activity when the actor simply performs the task.

As shown in Table 4, there is fairly good consistency in the pattern of changes of activity (with the exception of the cerebellum), although the range of tasks used is small. Parietal cortical activity decreases with training; this change has often been interpreted as reflecting participants' decreasing need to monitor the somatosensory feedback from their movements. The decrease in frontal activity as training progresses is consistent with COBALT; with practice, participants have less need to use the conscious mode, which is associated with frontal activity. As noted earlier, one study reported a direct correlation between a drop in frontal activity and a decrease in subjects' report for the need to consciously monitor the required motor response (Seitz et al., 1990).

Many of these studies have reported increases in activity in the striatum and supplementary motor area, which may be considered together, given their strong reciprocal connections.

 Table 4

 Summary of Changes in Brain Activity During Motor Skill Learning

Reference	Task	Cerebellum	Supplementary motor area	Striatum	Parietal	Frontal	Primary motor cortex
Friston et al., 1992	Explicit sequence learning	Ļ					
Jenkins et al., 1994 <sup>a</sup>	Explicit sequence learning	Ļ	1	Ļ	Ļ	Ļ	
Karni et al., 1995 <sup>b</sup>	Explicit sequence learning						↓ then ↑
Schlaug et al., 1994	Explicit sequence learning			1	t		
Seitz et al., 1990	Explicit sequence learning			Ť	ţ	ţ	
Seitz & Roland, 1992	Explicit sequence learning			1	Ļ	Ļ	
Seitz et al., 1994	Explicit sequence learning	t	1		Ļ	Ļ	1
Grafton et al., 1992	Pursuit rotor		Ť	Ť			Ť
Pascual-Leone et al., 1994 <sup>b</sup>	Serial response time						1
Doyon et al., 1996	Serial response time	Ť		ſ			

<sup>a</sup> This study compared different levels of training in different participants, rather than the same participants at different times in training. <sup>b</sup> These studies measured changes in the primary motor cortex only.

COBALT proposes that learning in the unconscious mode (such as that in the striatum) can be likened to a network being tuned. In neural network models, the greater part of learning (i.e., weight change) occurs during early trials, with steadily decreasing weight change on successive trials. It seems sensible to propose that greater learning is correlated with greater neural activity. Why, then, should there be an increase in striatal activity with training if the greater neural changes should, theoretically, be occurring in the early trials; and why does learning appear to occur first in parietal cortex? A possible resolution lies in the nature of sequences. Sequence learning differs from other types of learning in that the first presentation of a sequence is by definition indeterminate. The sequence may need to be presented a number of times before the regularities it presents are detected and learned. This is true whether the full sequence is learned or whether learning occurs by chunks within the sequence (Cleermans, 1993; Dominey, 1998; Keele & Jennings, 1992). Sequence learning can be contrasted with perceptualmotor integration learning, where the relationship to be learned (between an environmental goal and an egocentric spatial target) is consistent from trial to trial. It is notable that once a sequence has been learned, a change in the sequence leads to immediate change in activity in the striatum (Berns, Cohen, & Mintun, 1997), as is consistent with the idea that learning a sequence may take repeated presentations, but the striatum is indeed crucial to the representation.

# **Comparison With Other Theories**

Until this point, research on the neural basis of motor skill learning has been primarily empirical, and there has been little in the way of integrative theory. Although there are computational models (e.g., Saltzman & Kelso, 1987; Schoner, Zanone, & Kelso, 1992) some of which are neurally inspired (e.g., Dominey, Arbib, & Joseph, 1995; Fagg & Arbib, 1992) these models approach this problem at a different level of analysis and seek to account for the characteristic changes in behavior associated with learning.

COBALT seeks a broader account of the contribution of neural structures and the cognitive processes supported by these structures. Other researchers in neuropsychology working toward this goal have drawn conclusions about the role of specific structures in motor skill learning, although not as part of a general theory of motor skill learning. The predictions of CO-BALT may be compared to the predictions these researchers have made.

Striatum. The role of the striatum in motor skill learning has been the subject of much speculation. COBALT contends that the striatum is important for motor skills that demand sequencing, but other researchers have offered different accounts of the striatal contribution to motor skill learning.

Heindel and his associates (Heindel et al., 1988, 1989; Heindel, Salmon, & Butters, 1991; Paulsen et al., 1993) have suggested that the basal ganglia are important for motor programming and that deficits in motor skill learning are due to an inability to adjust motor programs. The term *motor program* refers to a plan for movement (Keele, 1981), so it is difficult for this explanation to account for the intact perceptual-motor integration skills that striatal patients show (e.g., Willingham & Koroshetz, 1993; Willingham et al., 1996).

Frith et al. (1986) have suggested that the striatal contribution may be to "motor set." It is not entirely clear what motor set is. It appears to refer to an ability to rapidly adjust to task demands, that is, to understand the requirements of a motor task. There is some evidence that striatal patients show particularly poor performance on the first few trials of a task, but their impairment is not limited to these trials; they show slow learning throughout training.

Flowers (1978) has suggested that striatal patients are impaired in making movements in the absence of strong cues in the environment to guide the movements (also called "openloop" movements). One might predict that these are exactly the type of movements necessary in sequencing skills, because improving in sequencing skills involves anticipating successive parts of the sequence. If striatal patients cannot prepare motor acts in advance of cues in the environment, this deficit may be the root of an apparent problem in motor sequence learning. Recent evidence indicates, however, that open-loop movements do not present a particular problem for striatal patients (Hocherman & Aharon-Peretz, 1994; Willingham, Koroshetz, Treadwell, & Bennett, 1995), whereas they are consistently impaired in motor sequencing, and so the interpretation of the deficit as one of sequencing seems preferable. Pascual-Leone et al. (1993) have suggested that the contribution of the striatum to motor skill learning is in its contribution to working memory. It is true that the striatal damage has an impact on working memory ability (Gabrieli, Singh, Stebbins, & Goetz, 1996), most likely through its interconnections with the prefrontal cortex, which is known to support working memory (Goldman-Rakic, 1995).

Pascual-Leone et al. (1993) have pointed out that working memory may contribute to learning of certain motor skills, in particular, sequencing skills. This assertion makes intuitive sense, because it seems that the components of a sequence would need to be active in working memory simultaneously for them to become associated. Still, whether working memory plays any role in motor skill learning is very much in doubt, with some evidence in neurologically intact participants indicating that it does (Cohen, Ivry, & Keele, 1990; Nissen & Bullemer, 1987) and other evidence indicating that it does not (Frensch, Buchner, & Lin, 1994; Stadler, 1995). Frensch and Miner (1994) reported correlations between measures of working memory and sequence learning, and these correlations were observed only when participants were distracted. They interpreted these data as showing that working memory becomes important to sequence learning only when working memory is taxed. Recent data show, however, that a secondary task does not affect sequence learning but does affect the ability to express sequence knowledge (Heuer & Schmidtke, 1996; Schmidtke & Heuer, 1997). Further, some patient groups with reduced working memory capacity are able to learn sequencing skills normally, for example, Alzheimer's disease patients (Ferraro et al., 1993; Knopman, 1991; Knopman & Nissen, 1987).

*Prefrontal cortex.* Two recent reviews of the neuroanatomy of motor skill learning make no mention of the prefrontal cortex (Halsband & Freund, 1993; Salmon & Butters, 1995), and indeed there has been little testing of patients with frontal lesions on motor skill learning tasks.

Deuel has reported, on the basis of lesion studies in monkeys, that the prefrontal cortex is crucial for sequence learning (Deuel, 1977; Deuel & Dunlop, 1979): Monkeys trained on a sequence of movements are impaired when they are trained to relearn the sequence after removal of the periarcuate cortex. It seems likely, however, that this apparent sequencing deficit is more likely a working memory deficit, because monkeys with similar lesions tested on similar tasks perform well if the environment provides cues as to the appropriate sequence; it is only if the monkeys must generate the sequence from memory that they are impaired (Pinto-Hamuy & Linck, 1965). Indeed, human patients with frontal cortical lesions are generally impaired in the temporal ordering of events (i.e., sequencing), but they are able to make sequential movements without difficulty if environmental cues make it clear what movements they are to make (De Renzi, Faglioni, Lodesani, & Vecchi, 1983). (This deficit may be compared to that of patients with damage to the striatum or supplementary motor area, in whom the deficit is clearly in sequencing the movements, not remembering the order; they are unable to sequence even two movements normally.) Perhaps most telling, recent reports have shown that patients with frontal lobe damage are able to learn the serial response time motor sequencing task normally (Marks & Cermak, 1996).

More recent functional imaging work has shown that prefrontal cortical activity is associated with performance of a finger

sequencing task (Jenkins et al., 1994; Schlaug et al., 1994; Seitz & Roland, 1992; Seitz et al., 1990). This finding has usually been interpreted as reflecting participants' need to mentally rehearse (presumably in working memory) the necessary sequence of finger movements. This explanation is not dissimilar to COBALT's contention that the frontal cortex is important in the conscious mode. The difference is that COBALT posits that the prefrontal cortex not only maintains the proper sequence in working memory, but actually directs the movements by selecting the spatial end-point targets when movements are made in the conscious mode. This contention is supported by other functional imaging results showing dorsolateral frontal activation during the selection of movements when participants are told to select any movement they like at random (Deiber et al., 1991; Playford et al., 1992), that is, when they would not need to maintain a particular sequence of movements in working memory. It is possible, however, that participants in such a task do maintain the last several movements they have made in working memory, so as to avoid repeating the same movements, in an effort to fulfill the requirement that movements be random. Dissociating a possible prefrontal cortical role in the maintenance of intended movements in working memory versus its possible role in directing intended movements will require further research.

*Primary motor cortex.* Lesion studies are not helpful in assessing the possible contribution of the primary motor cortex to motor skill because lesions there lead to paralysis. Several functional imaging studies have reported learning-related changes in the primary motor cortex. For example, Karni et al. (1995) asked participants to practice a sequence of finger-thumb opposition movements in daily practice sessions over the course of several weeks. They were scanned weekly by use of fMRI. The researchers reported an initial shrinkage of the area of activation caused by the sequence in the primary motor cortex, followed by a later expansion of the area of activation after more extensive training.

Although compelling, this study is difficult to interpret. Some studies that used Positron Emission Tomography have revealed an increase in primary motor cortex activity associated with learning (Grafton et al., 1992; Kawashima et al., 1995; Schlaug et al., 1994; Seitz et al., 1990) but others have shown no such increase (Friston, Frith, Passingham, Liddle, & Frackowiak, 1992; Jenkins et al., 1994). Pascual-Leone et al. (1994) reported that the size of cortical motor maps decreases once participants become aware of a sequence, but in the Karni et al. (1995) study, participants were aware of the sequence throughoutwhy, then, the increase? Note that the Pascual-Leone (1994) study measured only short-term change, immediately after participants became aware, whereas in the Karni et al. study measures were taken weekly. The activation initially dropped in the Karni et al. study, as is comparable to the results from the Pascual-Leone et al. (1994) study. The slow increase in activation may have resulted not from changes in primary motor cortex, but from changes elsewhere in the brain.

It is possible that the changes in activation Karni et al. (1995) report were the result of the increasing activity in other cortical regions, chiefly the supplementary motor area, that strongly project to the primary motor cortex; other areas were not imaged, and in the other studies showing learning-related changes in primary motor cortex activity, similar changes were observed in secondary motor cortical areas. Another possibility, suggested by Curran (1995, 1997), is that the primary motor cortex is associated with movement preparation. Learning occurs in other neural structures, but these structures communicate progressively earlier and more strongly with the primary motor cortex as learning progresses.

Cerebellum. There is no role for the cerebellum in motor skill learning in COBALT. The cerebellum has long been thought to play a central role in motor skill learning, with influential models proposed by Marr (1969) and soon thereafter by Albus (1971). These predictions that the cerebellum and closely related brain-stem structures participate in motor learning have appeared to be borne out by work showing that adaptation of the vestibulo-ocular reflex depends on the cerebellum and closely related nuclei (Ito, 1982; Lisberger, 1988). In related paradigms, human subjects have been found to be impaired in adapting to prism spectacles (Gauthier, Hofferer, Hoyt, & Stark, 1979; Weiner et al., 1983) and in learning to scale arm movements to visual feedback on a computer monitor (Deuschl, Toro, Zeffiro, Massaquoi, & Hallett, 1996). There is also good evidence of a cerebellar role in classical conditioning of the nictitating membrane response (Thompson, 1986) and of eyeblink conditioning in humans (Topka, Valls-Sole, Massaquoi, & Hallett, 1993). Human patients with lesions of the cerebellum or associated brain-stem nuclei are impaired in learning to trace a random figure (Sanes et al., 1990), and they fail to learn the repeating sequence in the serial response time task (Pascual-Leone et al., 1993). Functional imaging studies have shown cerebellaractivation associated with motor skill learning (Doyon et al., 1996; Grafton et al., 1994). In all of these studies, the authors have concluded that the cerebellum makes some contribution to motor skill learning in humans.

Evidence has been accumulating, however, that the cerebellum is not solely a motor structure (Fiez, 1996; Leiner, Leiner, & Dow, 1986, 1989; Schmahmann, 1991). The cerebellum receives direct projections from the frontal cortex (Middleton & Strick, 1994) and from the parietal cortex via the pons (Schmahmann & Pandya, 1989) and thus is anatomically situated to contribute to higher cognitive processes. Indeed, closer examination of cerebellar patients has revealed that they have a host of cognitive deficits, including deficits in generating words according to a rule (Fiez, Petersen, Cheney, & Raichle, 1992), solving the Tower of Hanoi puzzle (Grafman et al., 1992), visuospatial recall (Bracke-Tolkmitt et al., 1989), and initiation in recall (Appollonio, Grafman, Schwartz, Massaquoi, & Hallett, 1993), to name a few (for a review, see Daum & Ackerman, 1995). Functional imaging evidence also indicates that the cerebellum is active during tasks that have no motor component, (e.g., Gao et al., 1996; Kim, Ugurbil, & Strick, 1994; Parsons et al., 1995).

Of late it has seemed more difficult to find cognitive processes in which the cerebellum is not involved than to find those to which it contributes. A possible explanation is that the cerebellum contributes to attention, especially to the coordination of attention and arousal systems (Courchesne et al., 1994). Indeed, patients with cerebellar disorders are impaired in shifting attention (Akshoomoff & Courchesne, 1994; Courchesne et al., 1994). Ivry (1995) has reported a meta-analysis of imaging studies indicating that cerebellar activity is positively correlated with the difficulty of the task performed, as is consistent with a cerebellar role in attention. As Ivry has pointed out, it is also possible that task difficulty correlates with the number of possible responses that can be generated, and the cerebellum may play the strictly motoric role of preparing all of these responses, as some other brain system performs the high-level cognition necessary to select among these possibilities. This account is harder to reconcile with a recent demonstration that the cerebellum is active during a visual attentional task that places no motor demands on participants (Allen, Buxton, Wong, & Courchesne, 1997). In this fMRI study cerebellar activation was observed when participants watched a computer monitor while different colored shapes appeared and silently counted the number of times a particular stimulus appeared.

At this point, the strongest evidence for a cerebellar role in motor control comes from work by Ivry and his colleagues (e.g., Ivry & Keele, 1989; Ivry, Keele, & Diener, 1988) indicating a role for the cerebellum in timing. Ivry has argued that the cerebellum is involved in the timing of intervals across a number of domains, in both perception and action. For example, a patient may be asked to press a response key repetitively in time with a series of computer tones separated by a consistent temporal interval. The tones then stop, and the patient is to continue tapping at the set rate. In a perception task, the patient compares two temporal intervals, each interval specified by two brief tones. The patient is to select the shorter interval. The difference between the intervals is varied, and a perceptual threshold of temporal differences can be estimated. Cerebellar patients are impaired in both perception and production of temporal intervals (see Ivry, 1993, for a review; see also Harrington & Haaland, in press, for a different interpretation of these data).

In summary, it is clear from functional imaging and lesion studies that the cerebellum participates during motor skill learning tasks, but that its participation is central to the learning process is in doubt. The cerebellum may contribute some computation that is necessary across many domains of cognition, in particular, attention. Further, if the cerebellum does have a special function in motor skill learning, it is likely related to the timing of acts, not their spatial accuracy, and the current theory accounts only for spatial accuracy. Future versions of COBALT may include a role for cerebellar timing.

#### Evaluation

The neural separability principle, as instantiated in COBALT, makes specific predictions regarding the types of dissociations that should be observed given lesions to particular brain regions and regarding the patterns of activation that should be observed in functional imaging studies. Extant data regarding the locus of strategic learning, sequence learning, and perceptual-motor integration learning are consistent with COBALT. Other predictions have yet to be tested thoroughly. The theory predicts that the primary motor cortex and the cerebellum are not crucial sites of learning, and the research on these areas is ongoing. The prediction that learning the relationship between spatial targets and patterns of muscle activity takes place in the spinal cord is, as yet, untested.

# The Disparate Representation Principle

The disparate representation principle holds that three different representations are used in motor skill learning. The strategic process uses allocentric, conscious representations. The perceptual-motor integration and sequencing processes use egocentric spatial representations that are privileged to the motor system. The dynamic process uses representations of muscle activity. These assertions allow the following predictions: First, most motor skills examined in the laboratory rely primarily on sequencing or perceptual-motor integration processes (see Table 3) and therefore are represented in terms of egocentric space. Second, skills that are represented in egocentric space require that proprioceptive information be available during learning, because proprioception is crucial to developing egocentric representations. Third, learning by observation or by mental practice must be strategic learning, because proprioceptive feedback is not available under these conditions, and proprioception is essential for sequencing or perceptual-motor integration learning. Fourth, amnesic patients, who have a deficit in learning new explicit information, should be able to acquire strategic skills normally but show a deficit in applying their strategic knowledge after a delay, because such knowledge is represented explicitly.

## Representation of Learning

COBALT holds that sequencing and perceptual-motor integration skills are represented in egocentric space. Several predictions follow.

If these skills are represented in egocentric space, there should be excellent transfer among effectors for sequencing and perceptual-motor integration skills; such transfer is usually observed (Cohen et al., 1990; Imamizu & Shimojo, 1995; Keele et al., 1995; but see also Cohen, 1967). Indeed, one can produce handwriting that is recognizably one's own not only with the nonpreferred hand, but with a pen attached to one's elbow or foot, or clenched in one's teeth (Merton, 1972; Wright, 1990). Spatial accuracy is lower with the nondominant hand, however, as would be expected because of differences at the dynamic level; translation of egocentric targets into muscle commands should be less accurate with the less-practiced hand. A second prediction, therefore, is that skills that do not rely on changes in the dynamic process should show better intermanual transfer. There are limited data that directly address this point, but in the serial response time task actors simply press buttons, so the dynamic process contributes little to the learning; intermanual transfer is excellent in this task, as the theory predicts (Keele et al., 1995).

A number of researchers have directly addressed the question of how motor skills are represented. Are they represented in allocentric space, in egocentric space, in terms of muscle commands? Much of this research has focused on the serial response time task, and the results have not been consistent. Several attempts to address this question have been plagued by interference from explicit knowledge of the sequence used (Howard et al., 1992); a similar problem in a different paradigm was reported by Fendrich, Healy, and Bourne (1991). Some researchers have dissociated the spatial locations in which stimuli appear from the locations of responses by having participants respond to a stimulus attribute other than its location (Mayr, 1996; Willingham et al., 1989). One can manipulate the stimulus and response sequences to determine whether participants learn a sequence of locations on the computer screen (presumably in allocentric space) or a sequence of locations on the response

board (presumably in egocentric space). In one experiment they learned only the response sequence (Willingham et al., 1989), and in another they learned both sequences (Mayr, 1996)although, as the author has pointed out, what appears to be knowledge of locations of stimuli may in fact be knowledge of locations to which the eyes should move. In a recent experiment, I sought to eliminate some of the problems of previous research (Willingham, in press). I showed that if participants do not become consciously aware of the sequence, merely observing the stimuli does not lead to learning. Further, a change in the stimulus-response mapping between training and test sessions allowed for separate testing of knowledge of where the stimuli would appear on the screen and knowledge of where the next response should be made. Results showed that participants know the latter, but not the former. In summary, the preponderance of evidence indicates that motor skill learning in the serial response time task is not represented as knowledge of the sequence of stimuli (which are represented in allocentric space), but neither is it knowledge of which movement to make next (i.e., it is not effector-specific). Implicit sequence knowledge in a motor skill seems most likely to be knowledge of a sequence of locations to which one should respond (i.e., in egocentric space), whether the response is a key press or an eye movement.

# The Role of Proprioception

Proprioception is crucial for the selection of egocentric targets because proprioception provides information about the location of body parts, which is necessary for a description of egocentric space. But the location of the body can also be ascertained through vision, and experimental evidence about patients with disruption of proprioceptive information has shown that they can use vision effectively as a substitute for proprioception (Jeannerod, Michel, & Prablanc, 1984; Rothwell et al., 1982; Sanes, Mauritz, Dalakas, & Evarts, 1985). Reaching movements in these patients are disrupted when visual cues are unavailable and they are forced to rely on egocentric spatial cues (Blouin et al., 1993). In their everyday lives, such patients report a great deal of difficulty with exactly those motor tasks for which visual information is lacking or difficult to use because the differences in body positions are subtle (e.g., buttoning buttons, hand-writing; Marsden, Rothwell, & Day, 1984).

If motor skill learning relies on egocentric space, then disrupting proprioception, which contributes to egocentric spatial representations, should disrupt learning. The role of proprioception in learning has been a long-standing problem in motor skill learning. Early stimulus-response chaining theories proposed that the peripheral feedback generated by executing one movement served as the initiating condition for generating the next (e.g., James, 1890). Lashley (1951) argued that this arrangement was impossible because well-learned motor acts (e.g., expert typing) are performed so rapidly that proprioceptive information does not reach the brain quickly enough to be the trigger for a subsequent movement.

Work by Taub and his colleagues (Taub, 1976; Taub & Berman, 1968) seemed to support the contention that proprioception is not crucial to motor skill. They conducted a series of experiments in which they severed the dorsal roots of the spinal cord of monkeys at various stages of development. They found that with sufficient training, the monkeys could perform a number of complex motor skills, such as grasping, reaching, and climbing, although they seemed to lack the dexterity of normal monkeys.

One might conclude that proprioception is not necessary for motor skill learning, but that conclusion would be premature. First, Lashley's (1951) point does not apply to learning but to the performance of highly practiced skills. Second, Taub (1976) tested monkeys on skills that might arguably be "hard-wired" in the nervous system because of their importance to survival; Taub acknowledged that possibility. Recent tests using laboratory skills (e.g., learning to catch a food pellet as it drops) have indicated that skill acquisition is retarded or impossible if proprioception is disrupted (Pavlides, Miyashita, & Asanuma, 1993; Sakamoto, Arissian, & Asanuma, 1989). This latter finding is consistent with anecdotal reports of humans who lack proprioceptive input as a result of peripheral neuropathy. For example, Marsden et al. (1984) reported the case of such a patient who could drive normally, but when he bought a new car, he could not learn to drive it and was forced to sell it and return to his old car. In sum, the issue is not settled, but the proposal that proprioception is important for motor skill learning is consistent with extant data.

## **Observation Learning and Mental Practice**

The conscious mode also makes possible the imitation of other actors' successful motor behavior. When an actor tries to imitate the backhand slice of a professional tennis player, it is the conscious strategic mode that is employed. Further, most coaching tactics rely on the conscious mode. Typically, the coach describes something the actor should do differently. It may be a new environmental goal ("Hit more lobs"), a new egocentric target ("Don't take such a big back swing"), or a new sequence ("Don't let your head come up until after you follow through"). The actor then implements these goals via the conscious mode.

The proposal that proprioception is crucial to motor skill learning raises other questions, however, because there appear to be task situations in which actors can learn new motor skills without performing them, by observational learning or mental practice. *Observational learning* occurs when an actor's performance improves after having observed someone else perform a task (Bandura, 1986). A number of experiments have indicated not only that observational learning of motor tasks occurs, but that performing a task confers no special advantage over simply watching someone else perform it (Blandin, Proteau, & Alain, 1994; Vogt, 1995; see McCullagh, Weiss, & Ross, 1989, for a review).

*Mental practice*, defined as the covert rehearsal of a task without any overt movement, appears to be another situation in which motor skill learning takes place in the absence of movement. A great many studies have investigated the effects of mental practice (compared with physical practice or no practice) in the last 50 years, and a recent meta-analysis has shown a small but reliable effect of mental practice on learning (Driskell, Copper, & Moran, 1994).

There appears to be a paradox: Motor skill learning apparently requires proprioceptive feedback, and yet there is good evidence that learning can take place when proprioceptive information is not available (i.e., observational learning and mental practice). The dual mode principle resolves this paradox by proposing that the unconscious mode of learning requires proprioceptive feedback, but the conscious mode does not. This account is quite different from that of many other researchers, who have proposed that the processes involved in observational learning or mental practice are similar to those involved in actual practice (Adams, 1986; Carroll & Bandura, 1982; McCullagh et al., 1989; Richardson, 1967; Scully & Newell, 1985).

COBALT predicts that observation and mental practice should yield conscious, explicit knowledge, which should be more susceptible to forgetting than the unconscious knowledge that accrues from physical practice because this unconscious knowledge is the result of tuning the control process. Forgetting of this unconscious knowledge therefore occurs only if the process is retuned in a different manner. At least one study has shown that observation leads to performance levels equivalent to those acquired from actual practice immediately after training, but that after a delay, greater forgetting is observed in the observation group (Ross, Bird, Doody, & Zoeller, 1985). The effect of mental practice diminishes across retention intervals, and it diminishes more quickly than the effect of physical practice (Driskell et al., 1994).

Because mental practice and observation enhance performance through the conscious mode, rehearsal of tasks to which the strategic process can contribute should lead to performance improvement, but tasks to which the strategic process contributes little should benefit less. Driskell et al. (1994) reported a meta-analysis showing that mental practice is indeed more effective for tasks coded as more cognitive, and the effect of mental practice diminishes across retention intervals, and more quickly than the effect of physical practice.

It should be noted that Driskell et al. (1994) reported a small but reliable effect of mental practice (r = .166) even for physical tasks in their meta-analysis, contrary to COBALT's predictions. This residual effect may be the result of nothing more than motivation; the control groups in these studies often simply did nothing.

## Motor Skill Learning in Amnesia

Amnesic patients have profound deficits in explicit memory, but their ability to learn motor skills is almost always reported to be intact; this dissociation appears to be one of the more reliable in the neuropsychology of memory (for a review, see Gabrieli, in press). The present theory holds that some aspects of motor skill may depend on explicit memory, however; it therefore predicts that under some circumstances, amnesic patients should be impaired in motor skill learning.

A patient with amnesia due to medial temporal lobe damage but intact frontal lobes can successfully generate new environmental goals to improve on a motor skill so long as those goals remain in working memory. If there are a delay and a retest, normal participants retain these more successful environmental goals via explicit memory and perform well. Amnesic patients, however, forget the more successful environmental goals (because of the failure of explicit memory), and their performance is worse after a delay. Thus, amnesic patients should successfully learn motor skills in which strategic learning is important (e.g., prism spectacle tasks) but show forgetting after a delay commensurate with their explicit memory deficit.

Amnesic patients should also show a normal benefit from

observation learning if tested immediately, because what they have observed is in working memory, which is intact (Scoville & Milner, 1957; Squire, 1992). If there is even a brief delay between the observation and test on the task, however, amnesic patients should show little benefit of observation because using what has been observed relies on explicit memory, which is impaired in amnesia. Neither of these predictions has been tested.

#### Evaluation

Four predictions derived from the disparate representation principle have been described. There is limited direct evidence regarding the representations supporting the perceptual-motor integration and dynamic processes, but the sequencing process does appear to use egocentric spatial locations, as predicted. The theory also successfully accounts for the role of proprioception in motor skill learning, and it provides novel accounts of the mechanism for learning by observation and the effects of mental practice, and the circumstances under which they occur. The fourth prediction, regarding circumstances under which amnesic patients show motor skill learning deficits, has not been tested.

# The Dual Mode Principle

The dual mode principle holds that motor acts can be executed in either a conscious or an unconscious mode. In the conscious mode the strategic process generates the target end points for movement and sequences them; in the unconscious mode the perceptual-motor integration and sequencing process do so. The conscious and unconscious modes are available throughout training. The conscious mode usually leads to more accurate responses, but it demands more attention than the unconscious mode. Thus, an actor may switch between the conscious and unconscious modes, weighing the possible trade-offs of accuracy and attentional cost.

The dual mode principle allows the following predictions: First, conscious processes may participate in skill acquisition at any time, because the conscious and unconscious modes are available at all times. Conscious processes are not used only in the initial stages of skill learning. Second, learning of some types of skills may occur outside of awareness; that is, the conscious mode may never be invoked. But if an actor has useful explicit knowledge, he or she will use it via the conscious mode. So although one can observe a dissociation where there is performance benefit without explicit knowledge, the opposite dissociation-explicit knowledge without performance benefit-should not be observed. Third, the attentional demands of a task decrease only if and when an actor uses the unconscious mode. This situation usually occurs with increased training, but it is the use of the unconscious mode, and not training per se, that results in the decreased attentional demands. Fourth, an actor may use the conscious mode when the unconscious mode would result in greater accuracy. This is the mechanism behind the phenomenon of choking under pressure.

# Role of Consciousness Over the Course of Training

In other theories of motor skill learning, conscious processes are important early in training, as an actor encodes the rules and goal of the task, but this knowledge is not important to performance improvement after the first few trials (Adams, 1971; Fitts, 1964; Schmidt, 1976). COBALT also posits that the contribution of the conscious mode to motor skill learning is important to the early stages of learning a novel skill. Because the processes in the unconscious mode are rooted in processes of motor control, an actor must physically perform a task for learning to occur in the unconscious processes. But conscious knowledge may be acquired without performing the skill, and it can affect performance via the conscious mode. Thus, in the very early stages of learning, the actor makes use almost entirely of conscious, strategic knowledge, because the unconscious processes have had no opportunity to be tuned.

COBALT differs from other theories because it predicts that strategic processes are at work throughout training. Therefore, effective strategies, if discovered, should improve performance whenever they are discovered, and they should be implemented through the conscious mode. Given that COBALT also holds that the conscious mode can change performance rapidly, one should see rapid performance change in the middle of training, as an actor gains conscious knowledge. This prediction has been confirmed in two different task paradigms. Both in the serial response time task (Willingham et al., 1989) and in a tracking task with a complex mapping (Brooks, Hilperath, Brooks, Ross, & Freund, 1995), some participants learn via the unconscious mode and show gradual improvement, whereas others report gaining conscious insight into the sequence or the tracking rule in the middle of training and show rapid improvement.

## **Dissociations of Awareness**

The conscious and unconscious modes operate independently; one may operate in the absence of the other. It should therefore be possible to observe sequence learning or perceptual-motor integration learning in the absence of awareness. Actors should be able to learn without awareness that they are learning.

There have been many such findings reported over the past 15 years. Participants can learn a repetitive sequence in the serial response time task without being aware that they are learning (Nissen & Bullemer, 1987; Willingham et al., 1989), and they can show learning of a repetitive segment embedded in what appears to be a random tracking task (Pew, 1974; Salidis, Willingham, Sederberg, & Hollier, 1996). Perceptual-motor integration learning can also occur in the absence of awareness. In the prism adaptation paradigm used by Bedford (1989), participants pointed to light-emitting diodes in a dark room and were not told that the prisms distorted their vision. (They are told merely that it can be confusing to point in the dark.) Participants' pointing accuracy improved with training, although they were not aware that they were learning.

It has been argued that these reported dissociations are spurious (Perruchet & Amorim, 1992; Shanks & St. John, 1994). Critics have argued that a number of the studies have had methodological flaws, mostly centering on the certainty possible when claiming that participants are truly unaware. In a typical experiment reporting a dissociation, participants perform a task, and their task performance indicates that they have acquired some knowledge. They are later given an explicit test of that knowledge, and some of them perform at chance. The typical interpretation is that a dissociation of knowledge has been observed, but, as Shanks and St. John have pointed out, one must be certain that the two types of tests (performance and explicit) test the same information. There is nothing marvelous about showing different performance on two tests if they test different things. Shanks and St. John have also pointed out that the explicit test is usually retrospective; it is administered after the training, whereas the performance measure is taken concurrently with training. Thus, explicit memory may be worse simply because of forgetting. Perruchet and Amorim have pointed out that the dissociation logic requires that the performance measure and the explicit test both be quite reliable. If the test scores have noise inherent in them, some will be higher than participants' knowledge would justify and some lower, so one should expect that, by chance, some proportion of participants will appear to have no knowledge on the explicit test but some knowledge on the performance measure.

These issues are not yet resolved, and research on this topic is ongoing. The dual mode principle clearly posits that reported dissociations of awareness are not artifacts, and if they are demonstrated to be artifacts, it will pose a significant, if not fatal, challenge to the principle.

The dual mode principle also predicts that the opposite dissociation should usually not be observed. A participant acquiring explicit knowledge of a task during training should be able to make use of that knowledge via the conscious mode and show a performance advantage over a participant without explicit knowledge, given two conditions. The first is that the participant must recognize that the explicit knowledge he or she has is applicable to the skill situation. Thus, in many experiments that use the serial response time task, some participants spontaneously acquire explicit knowledge of the sequence and subsequently show faster response times than those without explicit knowledge (e.g., Willingham, in press; Willingham et al., 1989). On occasion, it has been reported that some participants acquire explicit knowledge without subsequent performance improvement (Reber & Squire, 1994; Willingham et al., 1989). It is possible that such participants slow their responses in order to allow more time to rehearse the sequence and thus appear to show no performance benefit; it is also possible that these participants do not have explicit knowledge that they believe is sufficiently complete to use to enhance performance. Participants in Reber and Squire's study could produce less than a third of the sequence. In a direct test of the role of explicit knowledge on performance, Curran and Keele (1993) explicitly trained some participants on the sequence before they performed the serial response time task, and those participants showed a marked performance benefit. In sum, it appears that when fairly complete explicit knowledge is acquired, a performance benefit follows in the serial response time task.

The second condition for a performance benefit from explicit knowledge is that the explicit knowledge must in fact be relevant to task performance. The theory is clear about what is relevant in this context. Sequencing and perceptual-motor integration learning are based on egocentric spatial information, and so explicit knowledge must be in that format, or easily translated into it. For example, suppose that participants were trained explicitly to learn the sequence that a target on a screen followed and were later required to track the target by using a joystick. The explicit knowledge would be represented in allocentric space, but it would be easily translated into egocentric space if the mapping between the screen and joystick were compatible. If the mapping were incompatible, strategic processes would be diverted to the mapping, and because strategic processes require attention, there would not be sufficient attentional resources to make use of the explicit knowledge. This prediction of COBALT has not been directly tested.

The prediction regarding the dual mode principle refers to explicit knowledge acquired relatively early in training. It is also possible for explicit knowledge to make performance worse, if an actor attempts to apply explicit knowledge to performance relatively late in training. This is the well-known phenomenon of choking under pressure, and it is described in more detail below.

# Attention Over the Course of Training

It is commonly appreciated that as one practices a task, there are fewer demands on attention. This phenomenon has been confirmed experimentally and examined over the past 20 years (Posner & Snyder, 1975; Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977), usually with visual search tasks. Tasks that are highly practiced to the point of demanding few attentional resources are called automatic tasks, and those that do demand attention are called controlled.

According to the dual mode principle, the conscious pathway demands attention but the unconscious pathway does not. When an actor first performs a task, the unconscious mode cannot be used effectively; the task must be practiced for the sequencing, perceptual-motor integration, and dynamic processes to be tuned to it. Therefore, the conscious mode is used almost exclusively. With practice, the unconscious processes develop task-specific knowledge so that the unconscious mode can be used. Thus the task demands less attention with practice. This change from the conscious to the unconscious mode is not necessarily abrupt; the conscious mode can be used or not used from trial to trial, or even within a trial, and so the transition to automaticity generally appears graded (MacLeod & Dunbar, 1988).

COBALT is not offered as a theory of attention or of automaticity, but it does appear to be consistent with the broadest trends in the role of attention in motor skill learning.

# Nonoptimal Use of the Conscious Mode: "Choking"

Choking under pressure may be defined as the paradoxical decrement in performance efficacy at just the moment when the actor wants most to perform well. This phenomenon is certainly well known to the athlete and musician, and it has been reproduced in the laboratory (see Baumeister & Showers, 1986, for a review), but it has proven difficult to account for. A number of researchers have sought to account more generally for the Yerkes-Dodson law, that is, the fact that the performance curve follows an inverted U shape as arousal increases. The Yerkes-Dodson law may explain choking if the desire to perform well leads to very high levels of arousal. Easterbrook (1959) accounted for the Yerkes-Dodson law by suggesting that as arousal increases, the actor uses fewer cues. At low levels of arousal both task-relevant and irrelevant cues are attended to, but as arousal increases the irrelevant cues are not attended to, and so performance increases. At still higher levels of arousal task-relevant cues are dropped from attention, so performance decreases. Humphreys and Revelle (1984) have suggested that the inverted U shape of the curve is a result of the combination of two monotonic processes: the process of identifying and responding to stimuli, which becomes more effective with increasing arousal, and short-term memory, which becomes less effective with increasing arousal. Neiss (1988) has pointed out two problems with making arousal the basis of an account of the Yerkes-Dodson law. The same level of arousal can either facilitate or impair task performance depending on why the person is aroused; a person who is angry may not perform the same way as one who is anxious, although physiological measures may not distinguish the two. Further, physiological measures of arousal do not always agree within an individual. Baumeister (1984) did not describe the problem in terms of arousal. He suggested that desire to succeed in a task causes the actor to focus attention on the process of performance; most tasks can be performed automatically (i.e., without attention), and so attending to the task amounts to interference.

According to COBALT, neither arousal nor attention is central. Increased motivation to perform well causes an actor to use the conscious mode, because it usually leads to higher accuracy. The desire to perform well may be generated by introducing an audience, a competitor, or a reward for good performance. Performance becomes worse rather than better, however, if the skill is highly practiced to the point that the unconscious pathway can guide performance more effectively.

COBALT posits that choking occurs only if use of the conscious mode leads to worse performance than use of the unconscious mode. This should be the case only if there has been some opportunity for the unconscious mode to learn—if the actor is a novice, there is no barm in using the conscious mode, because the unconscious mode has little or no task-relevant knowledge yet. Thus, skilled performers should be more susceptible to choking effects than novices; as noted above, early in training, explicit knowledge typically aids performance. That novices show less choking is supported experimentally (Kimble & Rezabek, 1992; Paulus & Cornelius, 1974; Paulus, Shannon, Wilson, & Boone, 1972). Caution must be exercised in interpreting such data, however, because this finding may be the result of a floor effect; novices perform poorly, and so their performance cannot get much worse.

COBALT also posits that use of the conscious mode should not harm performance if the task is very simple, because in that case use of the conscious mode is sufficient to support performance. In the context of the model, 'simple' tasks are those for which an explicit description of the spatial targets can be provided in egocentric space; thus, hitting a button is a simple task, because the egocentric target can be coded explicitly; a tennis forehand stroke is not simple, because one typically does not code the required movement in egocentric space (i.e., the trajectory of one's hand). There is evidence that easier tasks are less susceptible to choking effects, although even these tasks may be susceptible to choking effects if the pressure is extreme (Bond & Titus, 1983).

## Evaluation

Four predictions derived from the dual mode principle have been described. COBALT provides an account of the mechanism by which awareness may contribute to skilled performance at any time during training, and why the attentional demands of a task typically decrease with training. The theory also strongly predicts that learning can occur outside of awareness—a claim that some research has supported but that remains controversial. Finally, the theory also provides a new explanation for the phenomenon of choking under pressure that accounts for differences in susceptibility to the effect according to the actor's expertise. This finding has proven a challenge to other theories of the phenomenon.

# Conclusion

COBALT successfully accounts for many of the motor skill learning data in human neuropsychology, including the learning abilities and deficits of neurological patients and the results of functional imaging studies of neurologically intact participants. The theory is primarily neuropsychological, but it does make some important cognitive predictions concerning, for example, the representation of learning, the role of proprioception in skill acquisition, and mental practice. The theory may also be the first to provide accounts of the role of conscious processes in motor skill learning and how they interact with unconscious processes. Thus it describes how instruction such as coaching is integrated into motor skill learning—a topic that other researchers have noted is seldom addressed in this area (Newell, 1991).

The chief limitation of this theory is that it is restricted to accounts of spatial accuracy. As may be deduced from Table 2, the motor skill learning tasks that experimenters have focused on (and therefore the data that theories must account for) emphasize spatial, not temporal, accuracy. Timing is explicitly important only insofar as the actors are told to respond as quickly as possible. The only inclusion of temporal information in the model is in the sequencing process, which represents temporal order on an ordinal scale. But more precise temporal information on a ratio scale seems likely to be crucial for many motor skills, particularly those where the actor does not control the timing of the task (e.g., hitting a baseball pitch). Integrating such temporal information into the existing model is an important challenge for future research.

The model demonstrates the explanatory power of a model that focuses on the putative neurological components of complex abilities such as motor skill learning. A challenge for this and other models will be greater specification of the mechanisms within each of these components.

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