

David Rosenbaum

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INTRODUCTION

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How do we move? How do we walk, talk, sing, and smile? How do we perform on the athletic field, play musical instruments, craft tools and works of art? How do we learn to carry out these activities, and why are some of us better at them than others? What goes wrong when, through accident or disease, the ability to move is impaired? How can movement disabilities be restored or, better yet, prevented? And how can machines be made to carry out the tasks that most people (and animals) perform effortlessly?

As this list of questions suggests, understanding human motor control can have significant effects in a wide range of endeavors. This is hardly surprising given that movement occurs in virtually all walks of life. In sports, where rapid coordinated action can make the difference between victory and defeat, an understanding of motor control can allow for more victories or heightened levels of competition. In the fine arts, where performance on the stage or in the studio allows for aesthetic expression, understanding how we control the movements of our bodies can enhance the quality of expression as well as the training that leads to it. In medicine, where paralysis, lack of coordination, or weakness can sabotage the quality of life, rehabilitation can be improved through a deeper appreciation of the means by which the motor system functions. Finally, at home and in the workplace, the use of machines or appliances can be made safer or more efficient through the application of principles gained through motor control research.

Two fundamental questions lie at the heart of this field of study. One is how we control our movements; the other is how we maintain stability. Holding an object steady in changing wind conditions or standing still in a subway are tasks that demand stabilization. Without muscular control, such tasks would be hopeless—as hopeless, in fact, as moving. Because stabilization as well as movement must be achieved by the system we will be study-

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ing, we will not refer to it as the *movement* system or the *stabilization* system, but rather the *motor* system.

The word *motor* has some unfortunate connotations. One is that of machinelike rigidity. Conventional motors churn away monotonously, performing the same motions over and over again. By contrast, behavior is endlessly novel, at least under normal conditions. The novelty of behavior could only occur if the motor system allowed for the generation of continually changing patterns of muscle activity. It does so by relying on a rich configuration of neuromuscular assemblages that have evolved over millions of years. If you doubt the sophistication of the motor system, consider modern robots. These devices embody much of what we currently know about motor control, yet they can barely walk across uneven surfaces without toppling over, or engage in such mundane activities as tying a Boy Scout knot. Given the relatively mediocre performance of state-of-the-art robots, our ignorance of motor control is painfully obvious. A robot may run with motors—the other connotation of “motor” control—but the human body does not, at least not with conventional motors made of axles and magnetic coils. The motive forces for behavior are controlled in more subtle and sophisticated ways. Understanding how these forces are governed and physically realized can help us develop more effective robots. In addition, and perhaps more importantly, it can help us appreciate how we function as active, intelligent agents.

■ **PHYSIOLOGICAL AND PSYCHOLOGICAL EXPLANATION**

What does it mean to understand human motor control? What is to be understood, and what form should the understanding take? The answers to these questions are not obvious, for under normal circumstances movement and stability just seem to happen. When things work well, it is often unclear what their underlying components are. A hallmark of skilled performance, in fact, is that it occurs effortlessly. Thinking about motor skills can often prevent them from happening.

In *abnormal* circumstances skills may be disrupted. As a result of accident or disease, one's ability to move or stabilize the body may be drastically impaired. A wide range of motor disorders afflict people; many will be discussed here. Considering these disorders and the factors that cause them helps illuminate the substrates of normal performance.

It is possible to study the motor system in many ways. Understanding the physical components of the system is a task of *physiologists*—people who investigate the functions served by the physical structures of the body. Physiologists interested in motor control focus on *muscles, bones, and joints*, as well as the *nervous system*, the neural network that governs how muscles act. The practitioners who apply this information in the clinic include *neuro-*

ogists, who diagnose and treat ailments of the nervous system, *orthopedists*, who diagnose and treat disorders of bones and joints, *physical therapists*, who help restore motion and stability through behavioral rehabilitation, and *prostheticians*, who design and fit artificial limbs (*prostheses*) for people with amputations. Rudiments of motor physiology will be described in Chapter 2, *Physiological Foundations*.

Besides analyzing motor control in physical terms, another useful approach is *psychological*. This approach is described in Chapter 3, *Psychological Foundations*. Theories in psychology are not restricted to effects of personality, mental illness, or conscious thought. They also focus on mental *functions*—conscious or unconscious—underlying performance. Psychologists do not usually deny physical causes of behavior; in fact, they are usually pleased if their models find physiological support. However, the explanations that psychologists pursue usually do not require one-to-one mappings of identified biological mechanisms to behavioral or mental phenomena. Psychologists accept the fact that perception, thought, and action may emerge from the collective effects of many biological mechanisms. Identifying those mechanisms or the way they work is of less concern than understanding the emergent properties of the system as a whole.

Both for psychologists and for physiologists, four major problems occupy the core of motor control research. These are (1) the *degrees-of-freedom* problem, (2) the *serial-order* problem, (3) the *perceptual-motor integration* problem, and (4) the *skill-acquisition* problem. The next sections introduce each of these problems in turn.

■ **THE DEGREES-OF-FREEDOM PROBLEM**

Most physical tasks can be performed in an infinite number of ways. This has some advantages. One is obstacle avoidance (Cruse, 1986). If you need to reach for an object and there are obstacles in the way, it is helpful to have more than one way to reach for it. Another advantage is that the limbs that normally perform the task may not always be available for doing so. Holding a heavy package, for example, may make it impossible for you to turn on a light switch the way you usually do (with your hand). Nevertheless, you can turn on the light switch with your chin, even if you have never done so before. Similarly, if you need to write with a pencil held between your teeth (for example, to write a rescue note if you are held captive), chances are you can do so, and even preserve your normal writing style (see Figure 1.1). Students of motor behavior call the capacity to perform a given task in a variety of ways *motor equivalence*.

The capacity for motor equivalence is made possible by the many degrees of freedom within the motor system. The degrees of freedom in a system are the number of dimensions in which the system can independently vary. The joints of the arm have seven degrees of freedom. The shoul-

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- A Able was I ere I saw Elba
- B Able was I ere I saw Elba
- C Able was I ere I saw Elba
- D Able was I ere I saw Elba
- E Able was I ere I saw Elba

Figure 1.1 Handwriting achieved through different means: (A) With the right (dominant) hand; (B) with the right arm but with the wrist immobilized; (C) with the left hand; (D) with the pen gripped between the teeth; and (E) with the pen attached to the foot. (Reprinted from Raibert, 1977.)

der has three (it can move up and down, from side to side, and it can twist), the elbow has two (it can bend and it can twist), and the wrist has two (it can move up and down and it can turn from side to side).

If the degrees of freedom of the motor system bestow the advantages of obstacle avoidance and motor equivalence, why speak of a degrees-of-freedom *problem*? To see why, consider the simple act of touching the tip of your nose with the end of your right index finger. Perform this act before reading on.

In all likelihood, you touched your nose in a relatively efficient way. It is unlikely, for example, that you snaked your arm around the back of your head or that you extended your arm straight in front of you and then brought your finger back toward your face. These would have been odd ways of touching your nose, although they are possible. The fact that you selected a more efficient trajectory suggests that you somehow eliminated from consideration awkward or inefficient movement paths. This seems unremarkable until you recall that the joints of the arm have seven degrees of freedom, but the tip of your nose (or its location) has three degrees of freedom—its x , y , and z position in Cartesian coordinates. Thus without even considering the finger, which adds still more degrees of freedom, a problem arises in determining how to bring the tip of your finger to the tip of your nose. There are more degrees of freedom in the arm than in the target location. Consequently, there are an infinite number of ways of bringing the tip

of your finger to the tip of your nose. Thus the problem of selecting a path that brings the tip of your finger to the tip of your nose is mathematically underdetermined. Still, you instantly and effortlessly picked just one path. Understanding how you did this, and how you regularly perform other related feats (however mundane they may seem), is the degrees-of-freedom problem.

Efficiency

How can the degrees-of-freedom problem be solved? One kind of solution relies on movement efficiency. As I mentioned before, it is unlikely that you brought your finger to the tip of your nose by wrapping your arm around the back of your head. Apart from the fact that this would have taken longer than a more direct path, this indirect path would have gotten your arm into an awkward final position. Your wrist and shoulder joints would have been in extreme angles at the end of the movement. As a result, your ability to make a second, unanticipated response would have been impaired. In general, it is not a good idea to end a movement with the limb adopting extreme joint angles, just as it is generally not a good idea to remain near the edge of a tennis court after returning a shot to your opponent. By returning to mid-court in tennis, you are in the best possible position for returning the next shot that may come your way. Similarly, by having your arm in the middle of its range of motion at the end of a motor act, the movements you can perform with it next are maximally diverse (Cruse, 1986; Rosenbaum, 1989).

Another possible efficiency constraint is to move as smoothly as possible. One way to do this is to minimize jerk, the rate of change of acceleration. To understand what this means, consider Figure 1.2, which plots acceleration as a function of time. The slope of the curve is steep when jerk is high but shallow when jerk is low. Correspondingly, when jerk is high, curves relating velocity to time are highly peaked, but when jerk is low, curves relating velocity to time are bell shaped. (Recall that acceleration is the time rate of change of velocity, and velocity is the time rate of change of position.) Measuring the velocities of aimed hand movements shows that they are usually bell shaped, as would be expected if jerk (or more properly, mean squared jerk integrated over movement duration) were minimized. Based on this fact, it has been proposed that minimizing mean squared jerk is a constraint on motor control (Hogan & Flash, 1987). If the constraint is used, it helps reduce the number of movements that can be performed. In addition, it can boost efficiency because when jerk is high, large forces must be generated, and these can place high demands on muscle metabolic energy.

Minimizing mean squared jerk and avoiding extreme joint angles are just two possible constraints for movement selection. Other possible constraints include minimizing changes in muscle torque (Uno, Kawato, & Suzuki, 1989) and minimizing a variable related to muscle stiffness (Hasan,

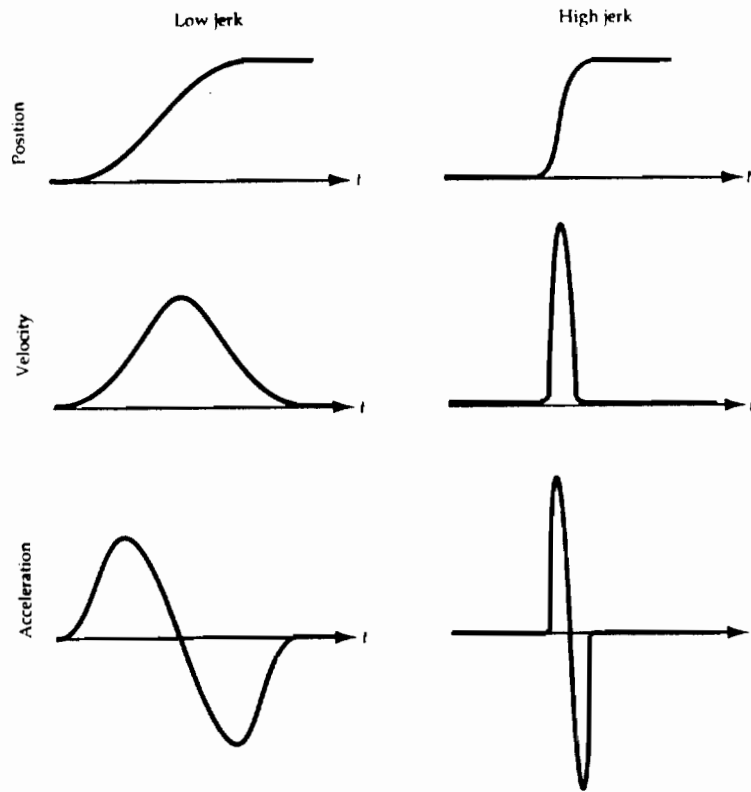


Figure 1.2 Position, velocity, and acceleration as a function of time, t , for a movement produced with low jerk and a movement produced with high jerk. Note that the absolute amplitudes of the velocity and acceleration profiles are higher for the high-jerk movement than for the low-jerk movement.

1986). Though there is debate about which constraints are actually used, the important point for now is that constraints for efficiency may help solve the degrees-of-freedom problem (Nelson, 1983).

Synergies

Another approach to the degrees-of-freedom problem is to suppose that there are dependencies between components of the motor system. Having such dependencies reduces the degrees of freedom that must be independent.

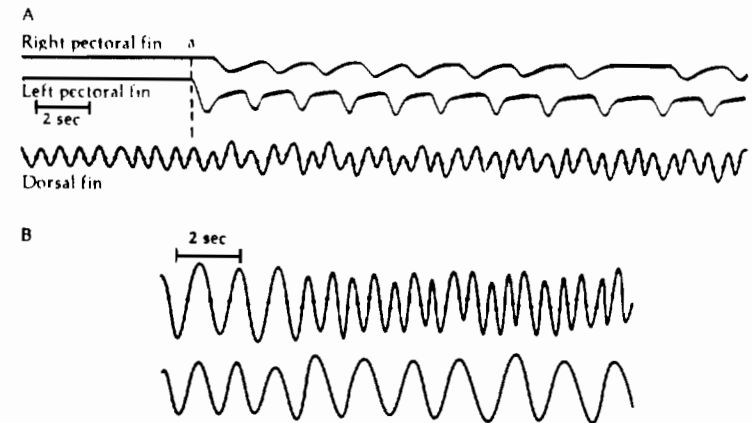


Figure 1.3 (A) The oscillation of a fish's dorsal fin changes when the right and left pectoral fins begin to oscillate. (B) In a person, when the right arm (upper curve) is supposed to oscillate at increasing frequencies, the left arm is affected. In both panels, the dots superimposed on the curves occupy equal time intervals. Thus variations in the dot positions along the vertical dimension indicate that the limb does not occupy the same position at the same time in the cycle. (From von Holst, 1939/1973b.)

cently controlled. This was the strategy advocated by Nicolai Bernstein (1967), the Russian physiologist who first identified the degrees of freedom problem.

A commonplace, if homely, example of a synergy is the tendency to blink during sneezing. This is a "hard-wired" motor interaction, in the sense that it occurs without our ability to control it. It illustrates how one kind of motor activity automatically dictates which other activities can or cannot occur.

Another example of a synergy is the difficulty encountered while rubbing the stomach and patting the head. In a formal experiment designed to evaluate this familiar difficulty, it was found that when people make rhythmic movements with two hands simultaneously, the frequency of one hand's movement influences the frequency of movement by the other hand (Gunkel, 1962). Dependencies between simultaneous movements also exist within individual limbs. The ability to flex and extend the wrist is aided if the elbow flexes when the wrist flexes and if the elbow extends when the wrist extends. If the elbow extends while the wrist flexes or if the elbow flexes while the wrist extends, the task is considerably more difficult (Kots & Syroveg, 1966).

Such interactions have ancient evolutionary origins, for the fins of a fish, like the arms of a person, are also coupled. Figure 1.3 shows interactions between the fins of a fish and interactions between the arms of a person

engaged in comparable activities (von Holst, 1939). For both organisms, the activity of one extremity has a pronounced effect on the activity of the other. Having dependencies like these frees us from having to "worry about" all the degrees of freedom that ultimately must be controlled.

Relying on Mechanics

The interactions just described are most likely based on the way nerve fibers are connected to one another. Recently it has been proposed that biomechanical factors alone can also simplify the degrees-of-freedom problem (Bizzi & Mussa-Ivaldi, 1989; Thelen, Kelso, & Fogel, 1987). A simple example is swinging the leg forward during walking—the so-called *swing phase* of locomotion. Detailed modeling of the behavior of the leg during the swing phase suggests that it can be achieved without concurrent muscle activation (McMahon, 1984). In other words, the trajectory of the leg during the swing phase need not be planned or controlled in detail but rather can be produced by taking advantage of the physical properties of the leg within the gravitational field. Thus the exact trajectory of the leg need not be planned explicitly, which implies further that the degrees of freedom that must be dealt with can be considerably reduced.

Muscle alone has mechanical properties that can be exploited to simplify the degrees of freedom problem. As will be seen in Chapter 6 (Reaching and Grasping), it has been useful to view muscles as springs whose resting lengths or stiffnesses can be set by the nervous system. (The resting length of a spring is the length to which it returns when no external force stretches or compresses it; the stiffness of a spring is the ratio of the tension it produces to the length it is stretched or compressed.)

An experiment in my laboratory (Rosenbaum, 1989) shows how the elastic properties of muscle may simplify movement planning. University students reached for a handle and turned it from each of a number of starting orientations to each of a number of target orientations. In analyzing how subjects chose to grab the handle just before turning it, we found that a simple "rule of thumb" accounted for their behavior (Figure 1.4). Subjects adopted relatively awkward arm postures when first grabbing the handle, but these postures ensured that by the end of the handle rotation the subjects' arms were always at or close to the resting position—with the right thumb pointing toward 11 o'clock. Thus subjects may have controlled their movements by treating their muscles (and tendons) like springs that could be "wound up" prior to movement and released to produce the needed movement. This strategy would have allowed elastic energy, stored in the muscles and tendons prior to the handle rotation, to be converted into kinetic energy during the rotation phase. If this is indeed what subjects did (albeit unconsciously), then they simplified the movement-planning problem by exploiting the mechanical properties of the muscles and tendons of their upper extremities.

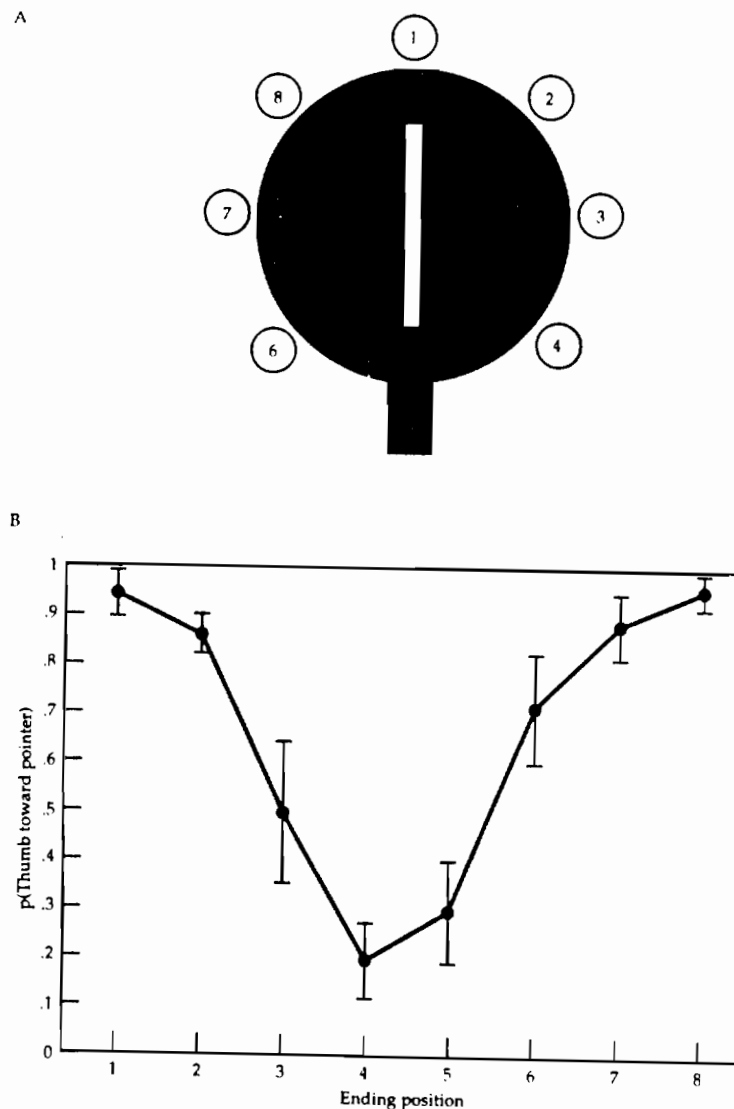


Figure 1.4 (A) Apparatus used in the handle-turning experiment of Rosenbaum (1989). A representative task was turning the handle so a tab initially covering target 5 would cover target 1 at the end of the rotation. (B) Probability of grabbing the handle with the thumb toward the lab as a function of the tab's ending position. The estimate of variability (± 1 standard error of estimate of the mean) for each point is based on starting position variability. (From Rosenbaum, 1989.)

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Path Planning, Inverse Kinematics, and Inverse Dynamics

A final remark about the degrees-of-freedom problem is that it is a problem at several levels (Jordan & Rosenbaum, 1989). At the highest level is the problem of *path planning*. A representative path-planning problem is deciding whether to reach to the right or left of a milk bottle to take hold of a cereal box. At a lower level is the *inverse kinematics* problem. This is the problem of converting the selected path into a time-varying set of joint angles. At a still lower level is the *inverse dynamics* problem—determining the forces to be produced in order to generate the desired joint angles. A considerable amount of work has been done on these problems in robotics and human motor control (Craig, 1986; Jordan & Rosenbaum, 1989; Saltzman & Kelso, 1987).

One of the most intriguing results from path-planning research is that people have a preference for straight-line hand motions. When asked to move the hand from one point to another on a horizontal surface, people are likely to move the hand in a straight line (Morasso, 1981). Even when people are asked to draw curved lines (which of course they can do), detailed analysis of their movements suggests that the curves they produce consist of series of straight-line segments (Abend, Bizzi, & Morasso, 1982). The finding that hand paths are often linear was first taken to suggest that path planning is done with respect to the Cartesian coordinates in which the hand moves, not with respect to joint coordinates. Later it was suggested that minimizing mean squared jerk could also give rise to straight-line hand trajectories (Hogan & Flash, 1987). Most recently, it has been suggested that minimizing torque changes at the joints can also yield straight-line hand paths and that this constraint accurately predicts deviations from straight-line paths (Uno *et al.*, 1989).

These three proposals have interesting implications for a general theory of motor control. The first proposal assumes that path planning is determined primarily by *geometric* constraints, the second proposal assumes that path planning is determined primarily by *kinematic* constraints, and the third proposal assumes that path planning is determined primarily by *dynamic* constraints. (*Kinematics* is concerned with motions without regard to the forces producing or preventing them. *Dynamics* is concerned with forces as well as motions.) The recognition that kinematics and even dynamics can affect path planning suggests that high-level aspects of movement planning do not occur in ignorance of the means by which plans must be executed. Apparently, low levels of control influence higher levels.

THE SERIAL-ORDER PROBLEM

Another major issue in the study of human motor control is how we control the *serial order* of our behaviors. The serial order of a set of elements is simply the sequence in which those elements occur. Thus *abc* has a differ-



Figure 1.5 Professor William Archibald Spooner. (Reprinted from Potter, 1980)

ent serial order than *acb*. When we engage in behaviors that have distinct elements, such as speaking, typing, or walking, the elements of the behaviors must be ordered correctly. Otherwise the behavioral outcomes would be maladaptive.

Speech Errors

As a case in point, consider Professor William Archibald Spooner, who taught at Oxford University in the late nineteenth and early twentieth century (see Figure 1.5). Professor Spooner made frequent speech errors. Typical examples were "The queer old dean" instead of "The dear old queen" and "You hissed all my mystery lectures" instead of "You missed all my history lectures." Although there is some question about the authenticity of these reports (Potter, 1980), there is no doubt that all of us make such mistakes from time to time. The errors mentioned above, which involve exchanging two speech sounds, are examples of *Spoonerisms*, named after the hapless professor.

What do speech errors tell us about the control of serial order? Suppose you said "We're going to the bootfall game" instead of the intended "We're going to the football game." Speech errors like this have been recorded in spontaneous conversation (Garrett, 1982) and in the laboratory (Motley, 1980). The error suggests that before you said the "f" that normally goes with "football," the "b" sound was available. Moreover, since the "b" sound exchanged with the "f" rather than, say, with the long "e" in "We're," the switch occurred in a nonarbitrary way. It is a general rule, in fact, that

consonants only exchange with other consonants and vowels only exchange with other vowels. Relatedly, though at a higher level of linguistic analysis, nouns tend only to exchange with other nouns and verbs tend only to exchange with other verbs.

Regularities of this sort suggest that there are distinct levels of representation in the planning and production of speech (Fromkin, 1973, 1980). For example, there is a level involving whole words, which respects their syntactic status (nouns versus verbs), and there is a level involving individual phonemes (see Chapter 9), which respects the distinction between consonants and vowels. Understanding how these levels of representation are used in speech production has been a topic of considerable interest among psycholinguists (Dell, 1986). More will be said about the modeling of speech errors in Chapter 9 (Speaking and Singing). For now, the important point is that the kinds of speech errors that people make indicate that speech is not simply produced by planning an utterance and then executing it, planning the next utterance and then executing it, and so on. Rather, there is usually a plan for an extended series of utterances and the words of which they are a part (Lashley, 1951).

Errors analogous to those in speech also occur in other domains of performance. Perhaps you have made the error of accidentally throwing a pair of dirty socks into a trash can rather than a clothes hamper (where you intended it). Or perhaps you accidentally poured catsup into your coffee rather than on the hamburger you wanted to flavor. Errors like these tend to occur when we are distracted, but they indicate that our bodily actions, like our speech, are based on plans that may have distinct functional levels. Pouring the catsup into the coffee indicates that part of the plan for pouring catsup includes the goal of emptying the contents into a suitable receptacle. The catsup-pouring error is not based on an inability to visually distinguish coffee cups from hamburgers. Instead, the problem arises because there is an abstract description of the task to be achieved (pouring) but the specifics of the task situation are momentarily misdefined. Analyses of such *action slips* suggest, therefore, that complex action patterns are assembled out of more basic schemas for action (Norman, 1981).

Coarticulation

Inferences about serial order are not only based on mistakes. Look into a mirror and say (rather deliberately) the word *tulip*. If you look closely, you will notice that your lips round before you say "t." Speech scientists call this phenomenon *anticipatory lip rounding*. Like the speech errors described above, anticipatory lip rounding suggests that a plan for the entire word is available before the word is produced. If "tulip" were produced in a piecemeal fashion, with each sound planned only after the preceding sound was produced, the rounding of the lips required for "u" would only occur *after* "t" was uttered.

Anticipatory lip rounding illustrates a general tendency that any theory of serial ordering must account for—the tendency of effectors to coarticulate. The term *coarticulation* refers to the simultaneous motions of effectors that help achieve a temporally extended task. In speech production, coarticulation occurs in anticipatory lip rounding, as we have seen, and in other aspects of speech as well. For example, *nasalization*, the passage of air from the lungs through the nasal cavity, often occurs before production of the consonant for which nasalization is required. In saying "freon," for example, nasalization often occurs during the first vowel, even though it is required only for the /n/. (Nasalization is made possible by lowering the *velum*, a fold separating the oral and nasal cavities.)

It does not suffice to say that coarticulation is simply governed by "low-level" physiological mechanisms, such as the activity of other articulators, for coarticulatory events are language dependent. In French, for example, where some words are distinguished by nasalization alone, nasalization occurs before /n/ but never so early that vowel identities (or word identities) are affected. By contrast, in English, where vowels typically are not distinguished by nasalization, lowering the velum often occurs in vowels (such as those in "freon") where it would not occur in French (Jordan, 1986). Results like these indicate that a theory of coarticulation (and so a theory of serial order) must account for psychological as well as physiological constraints.

Two final comments are in order about coarticulation. One is that coarticulation is not restricted to speech. Films of typists' hands reveal that both hands move continually during typewriting (see Figure 1.6). The fingers of each hand move toward their respective keyboard targets, even while other keys are being struck (Rumelhart & Norman, 1982). More will be said about this in Chapter 8.

Second, no matter how difficult coarticulation may be to explain, it is a blessing for us as behaving organisms. Think about a typist who could move only one finger at a time. Lacking the capacity for finger coarticulation, the person's typing speed would be very slow. Simultaneous movements of the fingers allow for rapid responding, just as concurrent movements of the tongue, lips, and velum allow for rapid speech. Coarticulation is an effective method for increasing response speed given that individual effectors (body parts used for movement) may move relatively slowly.

■ THE PERCEPTUAL-MOTOR INTEGRATION PROBLEM

Feedback and Feedforward

Consider once again the task of bringing the tip of your index finger to the tip of your nose. You may have noticed that, when you performed this task, your hand moved rapidly at first and then slowed down dramatically.

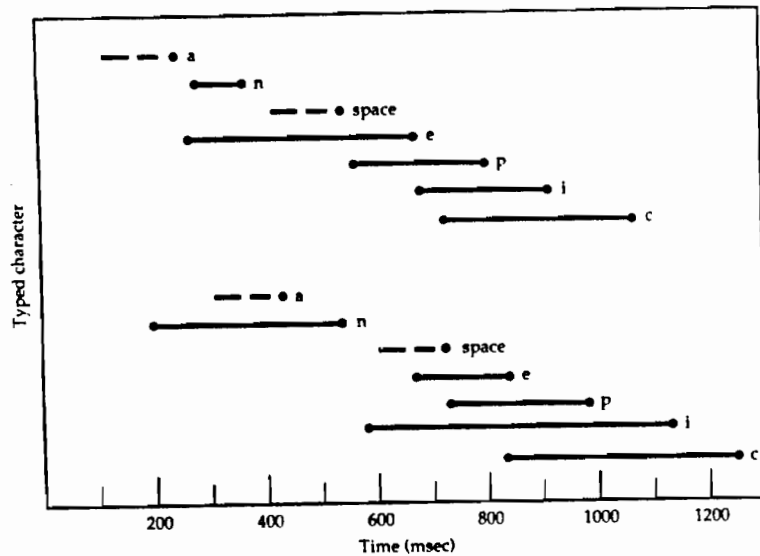


Figure 1.6 Coarticulation in typewriting. Though the "i" in "epic" is ultimately typed after the "e" and "p," it is initiated before either letter. Similarly, the first time "epic" is typed, the "e" is initiated before the "n" in the preceding word ("an"). The data were obtained from film records. (From Gentner, Grudin, & Conway, 1980.)

Virtually all aiming movements proceed in this two-stage fashion, with a *ballistic* phase followed by a *corrective* phase (Woodworth, 1899). Ballistic movements cannot be altered once they have been initiated. (Ballistic missiles, for example, cannot be steered once they are launched.) Ballistic movements are typically fast and cover most of the distance to the target. If the target has not been reached, corrective movements may then follow, using feedback to indicate the discrepancies to be overcome. Corrective movements, when they are effective, allow the distance between the effector and the target to be minimized.

When feedback is relied on effectively, corrective movements bring the effector closer and closer to the target until the distance to the target is acceptably small. This process is an instance of a negative feedback loop or *servomechanism* (see Figure 1.7). Servomechanisms have several components. The *reference signal* provides input to the loop about the target or goal state. In the case of bringing the hand to a target, the reference signal is a representation of the hand at the target. The *plant* is responsible for converting control signals into real outputs (for example, moving the hand). The *comparator* (the circled X in Figure 1.7) indicates the discrepancy between the sensed position of the effector and the reference signal. The *gain* (not shown in Figure

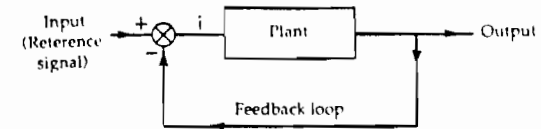


Figure 1.7 A negative feedback loop. (From Legge & Barber, 1976.)

1.7) transforms the discrepancy into a control signal that works to bring the sensed position closer to the reference signal, thus negating the error (hence the term *negative* feedback loop).

If bringing the hand closer and closer to a target illustrates the operation of a *negative* feedback loop, what is a *positive* feedback loop? If you have ever tried to cut your own hair, you probably have a good sense of what a positive feedback loop is. You may have tried to cut the hair on the back of your head while looking into a hand-held mirror in which you saw the reflection of your head in another mirror. Working in this miniature hall of mirrors, you may have discovered that every time you tried to bring the scissors closer to where you wanted them, they only moved farther away. This is an example of a positive feedback loop. The defining feature of such a loop is that errors increase rather than decrease when attempts are made to correct them.

Why is it so difficult to control one's movements when observing them through a double mirror? The answer is that the normal mappings between movements and their visual consequences are reversed. Even under such drastically changed conditions, we are nonetheless able to adjust our behavior, often in a relatively short amount of time (see Chapter 6). One of the most interesting problems in motor control research is how such compensations occur and why they occur as readily as they do.

Some additional terms are useful in connection with feedback processing. These are *closed-loop* control, *open-loop* control, and *feedforward*. Closed-loop control occurs when feedback can return to the comparator to be used for error correction. Seeing your hand as it approaches a visible target is an instance of closed-loop control. Here you can see where your hand is in relation to the target and make the necessary corrections based on vision.

Open-loop control occurs when feedback is unavailable. In open-loop situations, you get no information about the success or failure of your performance. As a result, your performance may fail dismally. Pointing at a moving target may be impossible, for example, if the position of the target cannot be seen, heard, or felt. Without feedback, the servo loop that normally allows you to point at the target has been opened (hence the term *open-loop control*).

There is an open-loop condition in which you can track a moving target reasonably successfully, however. This is when the target's motion is

predictable. For example, if your task is to point to a target that moves from one fixed location to another at a constant rate, it may be possible to point to the target quite well. The reason is that you can anticipate the target's position; your reference signal changes as a function of time. Such anticipation is called *feedforward*. Whenever performance is accurate though feedback is removed, it can be inferred that feedforward is being used.

Under open-loop conditions, a surprising number of movement sequences can be performed reasonably well. For example, monkeys deprived of sensory feedback from their limbs can walk and climb, though less gracefully than monkeys with sensory feedback (Taub & Berman, 1968). Similarly, a man who could not feel his body (shudder the thought!) because of a disease affecting his sensory pathways but not his motor pathways could draw complex figures on command, could sequentially touch his thumb with each finger of the same hand, and could touch his nose, all without the aid of vision (Marsden, Rothwell, & Dell, 1984). Abilities like these indicate that the gross features of some movements can be performed entirely under feedforward control. When these same movements are performed with feedback, they are performed more precisely.

Spatial Coordinates

Let us consider for one last time the task of bringing the fingertip to the tip of the nose. As we have seen, this task, when performed under normal feedback conditions, illustrates the operation of a negative feedback loop. Considering the nature of the error correction necessary for this task reveals another important aspect of the perceptual-motor integration problem. If your eyes are closed and your finger is not yet in contact with your nose, the error being reduced is the discrepancy between the felt position of your finger and the felt position of your nose. In order for this distance to be reduced, the felt positions of your finger and your nose must be referred to some common spatial coordinate system. Without such a common spatial coordinate system, your finger would wander aimlessly toward or away from the target, perhaps eventually touching it, but only by chance.

One of the issues to be resolved in the analysis of perceptual-motor integration is which spatial coordinate system is used for any given task. For the task of bringing the finger to the nose, it can be assumed that errors are defined with respect to a *body-centered* spatial coordinate system. That is, the "map" that must be used need not take into account where the body is situated in the external environment. On the other hand, the map must take into account the relative positions of the hand and nose. It would not suffice, for example, merely to know how far the finger is from the nose along the length of the arm, neck, and face, because this distance (measured along the skin) remains constant during the movement.

For other tasks, it may be necessary to assume that the spatial coordinates that are relied on are defined with respect to the external environment. As

an illustration, consider a study reported in 1938 by Wickens (reviewed in Gallistel, 1980). Subjects in this experiment held the hand palm-side down on a device that transmitted an electric shock to the fingertip. The shock was regularly preceded by a tone, and after a few exposures to the tone-shock pair, subjects withdrew their fingers from the shocker as soon as the tone was presented (but before the shock came on); to make the withdrawal response, subjects *extended* their fingers. The critical experimental manipulation occurred when subjects were asked to turn their hands over, leaving the palm up rather than down on the shocker. The question was what response subjects would now display after hearing the warning tone. Would they *extend* the finger, the muscle response they had previously displayed, or would they *flex* the finger, the muscle response that would bring the finger to the spatial position it had been brought to before? The answer was that they *flexed* the finger—the response that was muscularly opposite the earlier withdrawal response. Flexing the finger in the palm-up orientation was clearly adaptive given the unpleasantness of the shock. Evidently, the response that was learned was defined with respect to the spatial layout of the experimental apparatus, not with respect to the muscle movements that happened to be made in the first part of the experiment.

Another study leading to the same kind of conclusion involved a reaction-time procedure. Subjects in this experiment (Wallace, 1971) were asked to press a left or right button with their right or left hand (see Figure 1.8). The signals for the button presses were lights that appeared on the left or right side of a panel placed directly in front of the subject. In one condition (the *compatible* condition), when the left light came on, the left button was to be pressed, and when the right light came on, the right button was to be pressed. In the *incompatible* condition, the right light signaled the left button press and the left light signaled the right button press. Subjects were slower to respond in the incompatible condition than in the compatible condition.

In another set of experimental conditions, subjects crossed their hands, so instead of pressing the left button with the left hand and the right button with the right hand, they pressed the right button with the left hand and the left button with the right hand. The question was which relations would give rise to fast responses—the relations between the positions of the lights and the positions of the *buttons*, or the relations between the positions of the lights and the positions of the *hands*? The answer was that the locations of the buttons mattered more than the locations of the hands (Wallace, 1971; see also Brebner, Shephard, & Cairney, 1972; Reeve & Proctor, 1984). Subjects were faster to respond with the left button when the signal appeared on the left than when the signal appeared on the right and subjects were faster to respond with the right button when the signal appeared on the right rather than on the left. This was true even though the right hand pressed the left button and the left hand pressed the right button. Thus subjects behaved as if the important feature determining the speed of their responses was where the responses were made in space, not which part of the body happened to make the response.

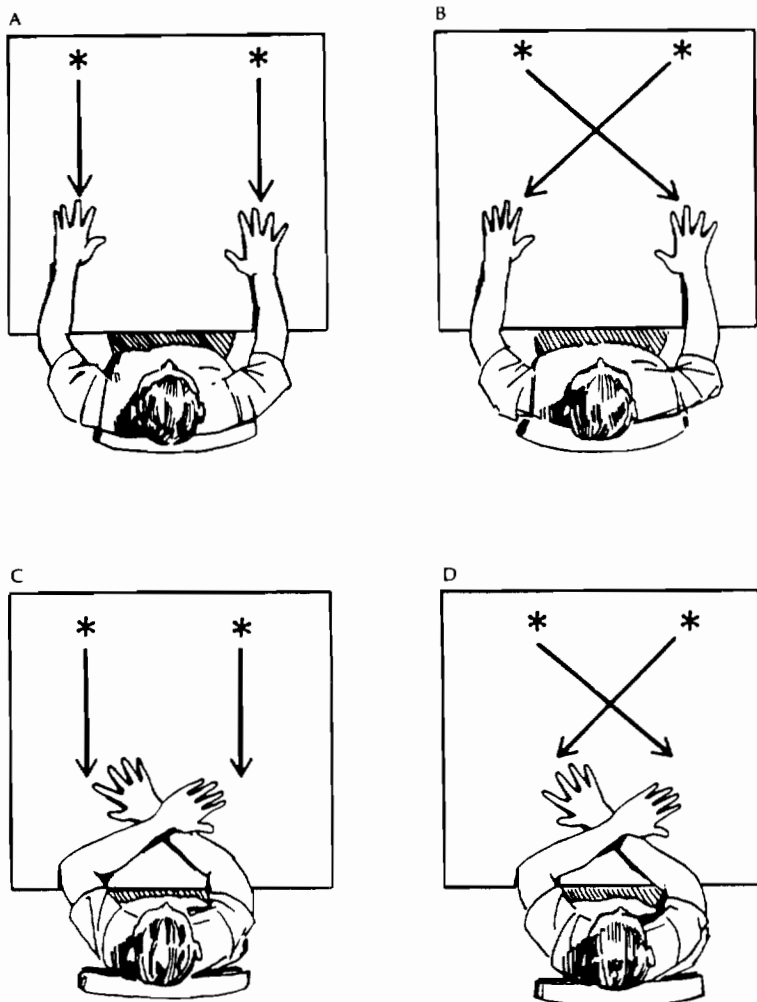


Figure 1.8 Four stimulus-response arrangements in Wallace's (1971) experiment. (A) Compatible mappings between stimulus locations and button locations and also between stimulus locations and effector (hand) locations; (B) incompatible mappings between stimulus locations and button locations and also between stimulus locations and effector locations; (C) compatible mappings between stimulus locations and button locations but not between stimulus locations and effector locations; and (D) compatible mappings between stimulus locations and effector locations but not between stimulus locations and button locations. Choice reaction times were faster in conditions (A) and (C) than in conditions (B) and (D).

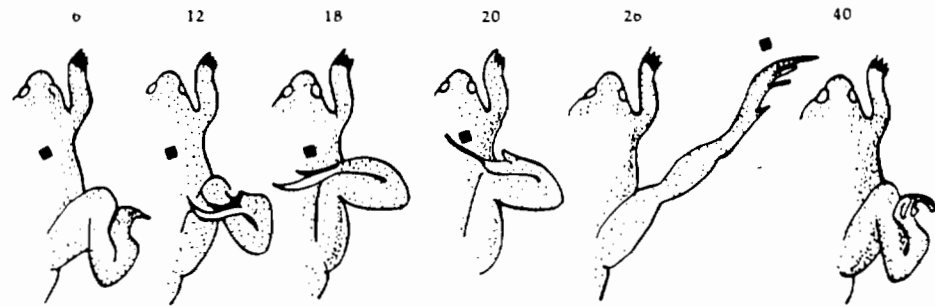


Figure 1.9 Wiping reflex in the spinal frog evoked by chemical stimulation (black square). The numbers at the top are film frame numbers. The movement was filmed at 48 frames per second. (From Berkenblit, Fel'dman, & Fucson, 1986.)

Results like these, which highlight the importance of spatial coding, will turn up throughout this book. One other study (Fucson, Berkenblit, & Fel'dman, 1980) is worth mentioning on this theme because of how beautifully it shows the fundamental nature of spatial coordinates in motor control. This study was done with frogs whose brains were surgically disconnected from their spinal cords (Figure 1.9). The experimenters applied a bit of irritating chemical to the skin of the frog and filmed the reactions that followed. Normally, frogs display a "wiping" reflex when treated in this manner. They reach for and whisk the irritated spot, just as they would wipe away a blade of grass or a fly that happened to land on their skin. Fucson *et al.* observed that the performance of the experimentally treated frogs was essentially the same as that of frogs with intact connections between the brain and spinal cord. As in normal frogs, even when the initial position of the frog's hindlimb varied and the location of the touch was unpredictable, the hindlimb maneuvered so it approached the irritation site from a propitious angle. The wiping motion that followed was remarkably accurate.

The coordination required for the wiping reflex is similar to that required for bringing the fingertip to the nose. The frog's ability to bring the end of its hindlimb directly to the irritated skin patch implies that within the frog's spinal cord are mechanisms capable of relating body positions within a single spatial map. Attributing this capability to the frog's spinal cord is not to trivialize the computations. The fact that brainless frogs can perform the wiping reflex implies that the transformations of sensory signals from the skin and limb into a spatial map, and the subsequent translation of those spatial coordinates into motor commands, are phylogenetically ancient capabilities.

Movement Enhances Perception

So far in this section on perceptual-motor integration, I have discussed the importance of feedback and feedforward for successful movement as well as

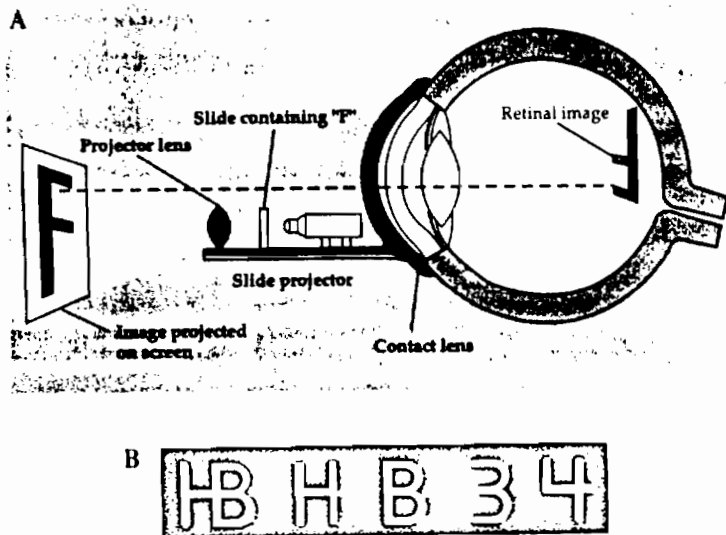


Figure 1.10 Retinal stabilization. (A) Overview of the method. (From Hilgard, Atkinson, and Atkinson, 1979.) (B) Disintegration of a retinally stabilized image over the course of time (left to right). From *Cognitive psychology and its implications*, by John R. Anderson. Copyright © 1980 by W. H. Freeman and Company. Reprinted by permission.

the significance of spatial coordinates. A common feature of the studies I have mentioned is that they demonstrate that movement benefits from perception. In this section, I show that perception also benefits from movement.

Movement never occurs in a behavioral vacuum. We move to be able to perceive, just as we perceive to be able to move. (Arguing which is more important, as some authors have, strikes me as a "red herring.") One reason perception benefits from movement is that movement allows for the transport of sensory receptors. We turn our eyes and our heads so we can take in visual information from a wide range of locations. We walk to new locations to see and hear what is going on there. We use our hands to feel objects or bring the objects to locations where we can inspect them further.

There are more subtle ways in which movement affects perception. Consider the visual effects of *retinal stabilization*. Here an image is projected onto the back of the eye (the retina) so that when the eye moves, the image goes with it (Pritchard, 1961). Usually when the eye moves, the image of a stationary object shifts across the retina. Images of moving objects also undergo some retinal slippage since visual tracking (following an object with the eye) tends to be imperfect (see Chapter 5). The question of interest in the retinal stabilization study is what happens when retinal slippage is eliminated.

The apparatus used to study retinal stabilization is shown in Figure 1.10. It consists of a contact lens attached to the cornea (the clear layer in the

front of the eye) with a tiny projection system attached to the lens. The projection system allows different images to be cast on the retina. It might be expected that with the image continually projected onto the same part of the retina, perception of the image would be clearer than usual. In fact, the opposite is the case. Within a few seconds, subjects see parts of the figure disappear. In the case of a letter, for example, first one stem disappears, then another, and then another (see Figure 1.10). Ultimately, the letter vanishes completely, though when a new letter is projected onto the retina, it can be seen, though it too fades in a piecemeal fashion after a short time. These results indicate that people become functionally blind to retinally stabilized images.

The fact that retinally stabilized images fade from view shows that the light-sensitive cells in the retina (photoreceptors) fatigue or adapt rapidly if they are continually stimulated in an unchanging fashion. The motion of the eye prevents this fatigue or adaptation.

Movement aids perception through means other than refreshing sensory receptors. People are more likely to identify a felt object correctly if they can explore the object actively with their hands than if the object is made to slide passively over the fingers (Gibson, 1962). Similarly, if people are asked to recall where their hands were positioned on a bar, they can recall the position better if they placed their hands in the position than if their hands were placed there by an experimenter (Paillard & Brouchon, 1968). These results indicate that the opportunity to move actively facilitates perceptual identification and memory.

Suppression Effects

Whereas the examples just described show that movement enhances perception, movement can also have the opposite effect. Look into a mirror and try to watch your eyes move. You cannot see them do so (Dodge, 1900). If you have a friend look at your eyes while you move them, he or she will be able to see them move. This shows that eye movements are not simply too quick to be seen.

Why can't you see your own eyes move? Perhaps the most intriguing hypothesis is that your brain suppresses the visual inputs that occur when your eyes move rapidly from one place to another (Volkman, 1976; see Chapter 5). There could be a distinct functional advantage of such *saccadic suppression*. (Saccades are the "jumps" of the eye that occur when you visually inspect a static scene or text.) Since the retinal image is smeared during saccades, the smear might not serve a useful purpose for perception and in fact could mask visual percepts obtained just before or just after saccades occur. Saccadic suppression could help reduce the damage to visual perception caused by such retinal smearing. (Chapter 5 provides a more extensive discussion and critical evaluation of this proposal.)

Suppression effects are not limited to eye movements. Chewing sounds are loud, yet we barely hear them. The reason is that during chewing there is internal suppression of auditory feedback (Rosenzweig & Lehman, 1982). Similarly, during active hand movements (but not passive hand movements), sensitivity to brief tactile stimuli is reduced (Coquery, 1978; Garland & Angel, 1972). Finally, though it is a lighthearted example, it is noteworthy that we cannot tickle ourselves. To get a good tickle, you must be tickled by a friend!

Suppression of sensory inputs during movement helps the nervous system filter out movement-based sensory changes. As will be seen in Chapter 5, the filtering helps us distinguish perceptual changes due to motion of the environment from perceptual changes due to motion of the self. The disambiguation occurs by "subtracting" perceptual changes from motor commands.

This subtraction process was first discovered through a remarkable experiment with flies (von Holst & Mittelstaedt, 1950; see Figure 1.11). The experiment was prompted by the observation that when a fly stands still and a drum with vertical stripes is turned around it, the fly turns with the drum, presumably to keep itself stationary with respect to the external world; this behavior is known as the *optomotor reflex*. However, when the stripes are stationary the same fly moves freely in front of them. The paradox is that the visual stimulus is approximately the same when the fly moves and the stripes are stationary as when the fly is stationary and the stripes move, yet only in the latter case does the fly reposition itself with respect to the stripes. Why does the fly turn with the stripes when the stripes turn but disregard the stripes when the stripes are stationary?

To find out, von Holst and Mittelstaedt twisted the fly's head 180° with respect to the longitudinal axis of its body and glued the head in this new position. The effect was to spatially interchange the left and right eyes. Under this condition, the fly's behavior was, to say the least, strange. When the fly stood still and the vertical stripes turned to the right, the fly turned to the left, but when the fly stood still and the vertical stripes turned to the left, the fly turned to the right. When the fly attempted to move on its own, it took a step one way or the other and then stood stock still, frozen!

How can these results be explained? The answer ascribes more intelligence to the fly than one might expect. According to von Holst (1973a), the fly "expects a quite specific retinal image displacement, which is neutralized when it occurs" (p. 179). In other words, when the fly turns to the right, it has a reference signal for a retinal displacement to the left, and when it turns to the left, it has a reference signal for a retinal displacement to the right. Obtaining the expected retinal displacement indicates to the moving fly that the world has in fact remained stationary. However, if the fly is stationary and the retinal image moves, the shift of the retinal image indicates just as clearly that the world has moved so, to keep its bearings, the fly makes a compensatory movement to realign itself with its surroundings. Finally, if

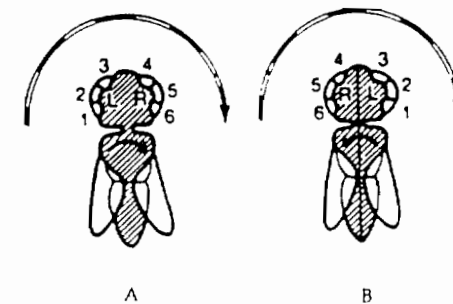


Figure 1.11 The behavior of a fly whose left and right eyes are in normal position (A) and whose left and right eyes have been interchanged by twisting its head 180° about the longitudinal axis of the body (B). Numbers designate eye segments. The arrow on the fly indicates the direction in which the fly is most likely to rotate given that the vertical stripes in front of it rotate to the right. (From Gallistel, 1980.)

the eyes are spatially interchanged, the expected and obtained retinal image displacements are reversed and the result, as von Holst and Mittelstaedt (see von Holst, 1973a, p. 179) put it colorfully, is a "central catastrophe."

Considering this behavior of the fly shows again how sophisticated the perceptual-motor system can be and at how early a stage of evolution this sophistication took hold. Not surprisingly, similar subtraction processes have been attributed to higher animals, including people (Sperry, 1950; von Holst & Mittelstaedt, 1950). More will be said about this process in Chapter 5.

■ THE SKILL-ACQUISITION PROBLEM

I have now discussed three of the four problems at the heart of motor control research: the degrees-of-freedom problem, the serial-order problem, and the perceptual-motor integration problem. One other problem remains to be summarized in this introductory chapter: how motor skills are acquired.

The problem of skill acquisition consists of several subproblems: (1) To what extent are motor skills innate and to what extent are they learned? (2) For those skills that are learned, how are they acquired? (3) Once a motor skill has been acquired, what is the nature of its underlying memory representation? More specific questions can also be added to this list: (4) As a motor skill develops, what changes in performance can be observed? (5) What is the role of feedback in learning motor skills? (6) What practice schedule is optimal? (7) How does the ability to learn or retain motor skills depend on the state of the learner, such as his or her age, neurological status, and motivation? (8) Is there an upper limit on the level of skill that can be achieved? (9) Is continued practice required to maintain skill levels? (10)

What factors determine how well one can transfer from one skill to another?

A section of Chapter 3 (Psychological Foundations) will be devoted to skill acquisition, so I will refrain from providing a detailed treatment now. Instead, I will describe one limited body of research that illustrates how skill acquisition can be studied effectively. This research captures some of the ideas about feedback processing that I have already introduced, although it concerns a relatively microscopic aspect of perceptual-motor behavior. Analyzing skill acquisition in detail is a formidable task because of the complexity of the problem. Therefore, it can be profitable to study "miniature" skills.

Modification of the Vestibulo-Ocular Reflex

Before reading further, perform the following task. Hold your hand straight in front of you, holding your thumb straight up. Keep your eyes on your thumb and rotate your head back and forth in the horizontal plane. As you do this, you will most likely notice that the visual image of your thumb remains crystal clear.

Now perform a complementary task. Hold your head still and swing your hand back and forth, holding your thumb erect. If you try to keep your eyes on your thumb, you will probably discover that you cannot see it clearly unless you rotate your arm rather slowly.

Why can you see your thumb more clearly when you turn your head than when you turn your arm? The answer is that different sources of information regulate your eye movements in the two situations. When your head is still and your eyes track your moving thumb, your eyes rely solely on visual error to keep the image of your thumb centered on your fovea (the part of the retina best adapted for fine pattern perception). By contrast, when you turn your head and try to keep your eyes on a stationary target, nonvisual feedback as well as visual feedback provide signals that help you maintain visual fixation.

The evidence for nonvisual feedback comes from experiments in which the head is passively rotated in the dark and the positions of the eyes are recorded. (Passive head rotation is usually achieved with a motor that turns an axle to which the head, or a helmet over the head, is attached.) Under these conditions, the eyes remain straight ahead when the head is rotated. Thus, the eyes counterrotate while the head turns, so the gaze is directed to the same location in the external environment. Since the eyes remain straight ahead even in complete darkness, their counterrotation is not based on visual feedback, but instead is based on vestibular feedback. Feedback mediated by the vestibular system concerns the orientation of the body or parts of the body. The vestibular system consists of structures within the inner ear that mechanically register accelerations in each of the three perpendicular dimensions (see Chapter 5, Looking). When the vestibular system is damaged, counterrotation of the eyes during head-turning is dis-

rupted (Bizzi, 1974). When the vestibular system is intact, the eyes begin counterrotating within 14 milliseconds (msec), or 14 thousandths of a second, of the start of head turning. This is too short for the eye movement to be based on visual feedback; the time needed for the eye to move in response to a visual stimulus is at least 100 msec (Lisberger, 1988). The eye's response to head rotation is therefore mediated by the vestibular system. The eye's response to head rotation is called the vestibulo-ocular reflex (VOR).

What does the VOR have to do with motor learning? First, it remains exquisitely precise over the course of growth and aging. A measure of the precision of the VOR is its gain, the speed of eye movement divided by the speed of head movement. A gain of 1.0 indicates perfect compensation, and this is the value that is normally recorded. Because gains of 1.0 are obtained in organisms whose nerve and muscle tissue have grown and undergone normal wear and tear, the VOR must change as a result of experience.

Just how changeable the VOR is has been demonstrated in experiments where magnifying or minifying lenses are placed over the eyes, causing images appearing on the retina to expand or contract. The lenses alter the speed at which visual images appear to move when the head turns. Magnifying lenses increase the apparent speed of image displacement, and minifying lenses reduce the apparent speed of image displacement. The consequence of magnification or minification is that the normal gain of the VOR is initially too small or too large. For example, when lenses double the image size, the speed of image displacement doubles, so the optimal gain for the VOR becomes 2.0 rather than the normal 1.0. After a few days of wearing such magnifying lenses under conditions of normal illumination, monkeys tested in the dark have gains close to 2.0, implying that the VOR adapts fully to the new relation between eye movement and image displacement. When minifying lenses are worn, the opposite effect is obtained. After wearing lenses that shrink images to one-quarter their normal size, the gain of the VOR approaches .25 (Lisberger, 1988).

For the gain of the VOR to change, the subject must be exposed to visual input and head rotations simultaneously. Wearing the lens with the head held stationary does not lead to adaptation, nor does moving the head in the dark. It is as if the nervous system learns to correlate head rotations with eye movements, based on the retinal image displacements that accompany head rotations. If the head rotations and retinal image displacements do not occur simultaneously, the correlations between them cannot be reevaluated (Lisberger, 1988).

What mechanism allows for changes of VOR gain? One way to find out is to study the times during eye counterrotations when recalibration effects appear. The first response to head-turning occurs 14 msec after the head starts to turn, as noted earlier. This delay remains unaffected by lens exposure. However, by 19 msec after the start of head-turning, experience-based changes in compensatory eye movements can be detected (see Figure 1.12). These results suggest that there are three components to VOR adaptation: (1)

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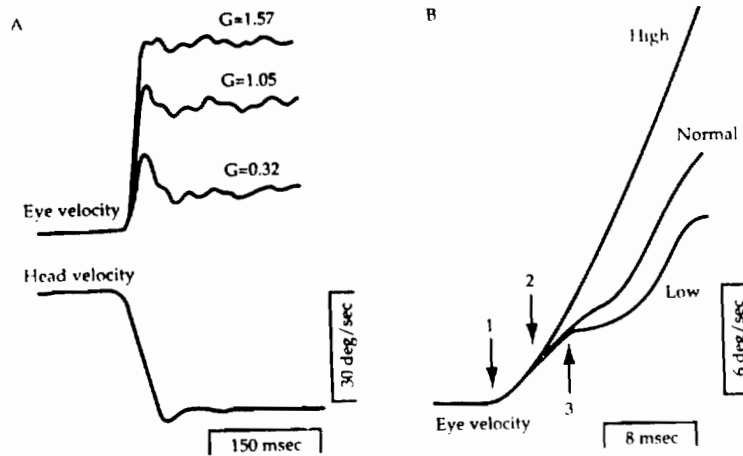


Figure 1.12 Change in monkey eye-movement velocity during head turns after exposure to magnifying lenses that increase the gain from 1.05 (the pretraining value) to 1.57 or after exposure to minifying lenses which decrease the gain from 1.05 to 0.32. (A) Slow-sweep records, showing the relation of the eye movements to head movements. (B) Fast-sweep records, showing the initial, immutable eye-movement trajectory, which begins at time 1, followed by the experience-based change in gain, first apparent at time 2 for the high-gain state and at time 3 for the low-gain state. (From Lisberger, 1988.)

an immediate, unchanging response; (2) a delayed, changing response; and (3) a capacity for introducing changes to subsequent responses based on the outcome of previous eye-head movements. Detailed work on the neurophysiological underpinnings of the VOR has shown that distinct neural pathways are responsible for these three functions and that the three pathways work in parallel. (It would be premature to identify these pathways now, since the rudiments of neuroanatomy have not yet been introduced.) The broader lesson is that even for a response system as simple and "mechanistic" as the VOR, complex neural subsystems come into play, with distinct functional responsibilities associated with each of them. One system acts automatically and immutably. Another acts rapidly but can be changed through learning. A third tunes the second based on feedback. As will be seen later, similar three-part schemes for motor learning and control have been identified in other, more complex skill-learning systems.

■ ORGANIZATION OF THE BOOK

Just as it is useful to have a plan for a series of movements, it is useful to have a plan for reading a book. The organization of this book is as follows.

As I have already indicated, Chapters 2 and 3 (which conclude Part

I) are concerned with physiological and psychological foundations, respectively. The bulk of the book (Part II) is organized by activity. Chapter 4 is concerned with walking and related forms of locomotion. Chapter 5 is concerned with looking and the control of eye and head movements. Chapter 6 focuses on reaching and grasping. Chapter 7 treats the control of writing and drawing. Chapter 8 covers the control of typewriting, piano playing, and other finger-movement tasks, which I refer to collectively as keyboarding. Chapter 9 pertains to the control of speaking and singing. Chapter 10, the last chapter in Part II, is concerned with smiling and other forms of facial expression.

Devoting a separate chapter to each of these classes of activity has several advantages. One is that research in motor control, like research in most fields today, has become rather specialized. It is not really a caricature of the field to say that there are people who work entirely on eye movements, others who work entirely on reaching and grasping, others who work entirely on speech, and so on. Judging from the specialized journals and meetings that exist for these subdisciplines, one might be led to conclude that the questions pursued in one have little or nothing to do with the questions in another.

The proliferation of subspecialties within motor control derives partly from the practical and theoretical interests of workers in the field. Practical concerns with particular tasks sometimes compel investigators to pursue those tasks at the expense of others. A researcher working for a typewriter company, say, is naturally more interested in keyboarding than singing. Theoretical interests also place some investigators on circumscribed research paths. Students of vision, for example, are naturally more interested in oculomotor control than in speech, just as researchers concerned with linguistics are more concerned with speech than with the control of eye movements. Because particular tasks rather than motor control as a whole may continue to interest many individuals, I have organized Part II so that any given chapter can be read on its own.

My second reason for devoting separate chapters to separate activities is that many specialty areas have developed their own problems and methodologies. The twists and turns within one area do not always map easily onto the issues in another. Rather than risk losing the richness of particular areas of study, I have decided to pay each area its due by considering it on its own.

In treating the subsystems separately, it is critical that the treatment not become too parochial. Therefore, areas of common concern will be highlighted as such, as will work focusing on coordination of different motor tasks. Being on the lookout for similarities among motor subsystems also puts us in an advantaged position for detecting differences among them. That there might be significant differences is a real and intriguing possibility, given that some information-processing functions may be controlled by independent modules with their own rules of operation (Fodor, 1983). If mod-

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ularity applies to the motor system, different motor activities might be controlled in wholly different ways. Treating the motor activities separately should allow us to identify these differences if they exist or to note their absence when they might be expected. (There are other defining features of modularity which need not concern us at this time.)

The final part of the book (Part III) is concentrated into a single chapter (Chapter 11, Conclusions). Here I offer some generalizations about motor control based on the preceding chapters. I consider in some detail two tasks that require coordination of several motor activities (eye-hand coordination and hitting an oncoming ball), I briefly review work on individual differences, and I discuss some promising new lines of investigation.

A final comment about the organization of the book concerns its title, *Human Motor Control*. Most but not all of the studies that I will describe have been done with humans, and many but not all of the activities that I will discuss can only be carried out by people. I have therefore included the word *human* in the title, though I will introduce animal research throughout the volume because of its enormous importance for the field at large.

My reason for using the term *motor control* also requires some justification, for some may feel it is a mistake to claim there is a system responsible for motor activity, separate from the systems responsible for perception or cognition. I make no such claim, however. What I do believe is that the control of movement and the control of stability can be properly viewed as distinct *functions*, or *sets* of functions, achieved by the nervous system. Demarcating neural control systems for analytic purposes does not imply a belief that the systems are isolated from one another. It is reasonable, and I believe helpful, to regard motor control as a topic for study in its own right, just as it is helpful to analyze perceptual function (for example, vision or audition) on its own.

Considering what we know about motor control is both gratifying and humbling. It is gratifying because great strides have been made in the past few years and hopefully will continue to be made in the near future. It is also humbling because so many challenges lie ahead. For all that we know about motor control, many questions remain. My fondest hope is that as you read this book, you will feel inspired to answer the questions that I raise as well as the questions you raise yourself.

■ SUMMARY

1. Motor control is essential for virtually all aspects of life. It allows us to communicate, manipulate objects, transport ourselves from place to place, eat, breathe, and reproduce. The central issues in motor control research are twofold: (1) How do we make movements, and (2) How do we maintain stability?

2. Two principal kinds of analyses have been pursued in the study of human motor control. One is tied to the physical mechanisms responsible for movement and stability. This sort of analysis has been pursued chiefly by physiologists. The other kind of analysis is concerned with functional aspects of motor control and can be carried out without necessary regard for the physical underpinnings of behavior. This sort of analysis has been pursued chiefly by psychologists.

3. One of the major issues in the field of human motor control is the *degrees-of-freedom* problem. The question is how particular movements are selected given that there are more degrees of freedom in the muscles and joints than in the description of the task to be performed. One way of solving the *degrees-of-freedom* problem has been to propose that *efficiency* is taken into account in selecting movements. One possible efficiency constraint is minimizing mean squared jerk. (Jerk is the time rate of change of acceleration.) Another approach has been to identify motor *synergies*—dependencies among effector elements, seen, for example, in the functional coupling of the two arms. These dependencies effectively reduce the degrees of freedom that must be controlled. A third approach is to rely on the *biomechanical* properties of the motor system. By relying on the effects of gravity, for example, or on the effects of the elasticity of the muscles and tendons, it may be unnecessary to compute detailed aspects of movement trajectories.

4. The *serial-order* problem—determining how movements are sequenced—is another central issue in motor control research. Errors in speech and other activities indicate that movement sequences are governed by complex plans with distinct levels of representation. The existence of plans is suggested as well by analyses of *coarticulation*—the concurrent activity of distinct effectors subserving temporally extended tasks such as speaking and typewriting. An example of coarticulation is anticipatory lip rounding during pronunciation of the word *tulip*.

5. Understanding how we coordinate motor activity and perception lies at the core of the *perceptual-motor integration* problem. Feedback processing provides an important illustration of perceptual-motor integration. When feedback loops are closed, it is possible to respond to feedback, but when feedback loops are open, behavior is ballistic and can be controlled only as well as feedforward (anticipation) allows. A negative feedback loop allows for error reduction based on feedback, whereas attempts at error correction in a positive feedback loop generally result in increased rather than decreased error.

6. Much of motor performance is organized with respect to the spatial coordinates of the body or the spatial coordinates of external space. The importance of spatial coordinates has been demonstrated in studies of learning and in studies of stimulus-response compatibility. The motor system aids perception by moving the sensory receptors. Eliminating the visual effects of

eye movement by stabilizing retinal images causes visual percepts to vanish. The motor system also aids perception by serving as a vehicle for active exploration of the environment, as when one actively explores an object with the hands. Perception can also be *suppressed* by motor activity, as in saccadic suppression. Some suppression effects are achieved by "subtracting" expected perceptual consequences from the perceptual consequences that occur when movements are actively generated. Even flies behave in ways consistent with this hypothesis.

7. The *skill-acquisition* problem is the fourth major issue in the study of motor control. A system that has been used to study this problem is the vestibulo-ocular reflex (VOR), which is manifested in the tendency of the eyes to maintain their line of sight as the head turns. After wearing magnifying or minifying lenses for a few days, the *gain* of the VOR (the ratio of eye speed to head speed) changes. Three subsystems seem to underlie the adaptation. One is rapid and unchangeable. The second is a bit slower and can be modified. The third brings about major gain changes based on feedback.

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PHYSIOLOGICAL FOUNDATIONS

■ INTRODUCTION

Movements are made in response to a variety of signals—external ones (a traffic light changing from red to green, the sound of a car horn, a thumb tack stepped on accidentally) and internal ones (a suddenly remembered appointment, an impulsive thought, a deep sentiment). Some movements are automatic whereas others are deliberate. Withdrawing the hand from a hot stove is usually an automatic act. Giving a downbeat to a symphony orchestra is usually carried out with more deliberate control.

No matter what the signal or the context for movement, virtually all movements involve the participation of large numbers of muscles (see Figure 2.1). If we had to think about all the muscles involved in motor performance, we would probably be unable to move skillfully or with enough time or energy left over for other tasks. The main challenge in the study of motor physiology is to understand how, from a physical standpoint, we can move as adaptively and effortlessly as we do.

The principal way that the nervous system allows for skilled motor performance is with special-purpose mechanisms. At the lowest levels are sensory receptors and muscle fibers. These structures are connected through a variable number of synapses (gaps between neurons). Some of the connections involve only a single synapse (*monosynaptic* connections). Others involve many synapses. Because only a few synapses are required for some connections, some responses to perceptual inputs are extremely rapid and automatic. The patellar tendon tap, in which the physician taps on the tendon just below the knee and the leg lifts, is a familiar example.

Pathways running through the spinal cord allow for communication between the peripheral and central nervous systems. Ascending spinal

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stimulus was presented. Apparently, people *can* accurately estimate times of brain events. They become aware of their own intentions only after a significant amount of neurological activity allows those intentions to coalesce.

■ SUMMARY

1. The central aim of motor physiology is to understand how the physical makeup of the nervous system and the musculoskeletal system allows for the adaptive control of posture and movement. Specialized mechanisms allow motor control to be carried out such that attention to the detailed properties of muscle activity is generally unnecessary.
2. Muscles contract when stimulated at neuromuscular junctions and stretch when subjected to mechanical loads.
3. The tension developed by muscle during active contraction is an inverted U-shaped function of muscle length. The shape of the function is due to the strength of actin–myosin bridges at different muscle lengths.
4. A motor neuron and the muscle fibers it innervates comprise a motor unit, the most basic element of motor control. It is impossible to contract voluntarily some, but not all, of the muscle fibers within a motor unit. With feedback, however, it is possible to activate a single motor unit. Motor units tend to be recruited in an orderly size-dependent fashion. Units containing small muscle fibers are generally activated before units containing large muscle fibers.
5. Muscle spindles are attached to the large muscle fibers (extrafusal) that produce adequate force to move a limb. Muscle spindles contain small fibers (intrafusal) that also contract. The sensory nerve fibers attached to muscle spindles respond to differences in the length of the muscle spindle and the length of the extrafusal. These sensory fibers serve as muscle stretch receptors. The signals they produce can be consciously perceived.
6. Sensory receptors in muscle tendons (Golgi tendon organs) tend to fire when muscle tension increases. The response properties of Golgi tendon organs are roughly opposite the response properties of muscle spindles: Golgi tendon organs fire when muscles contract, whereas stretch receptors fire when muscles lengthen.
7. Sensory receptors in the joints fire primarily at extreme joint angles. They may provide a warning signal about awkward or dangerous postures.
8. Sensory receptors in the skin (cutaneous receptors) are vital for precise manipulation, particularly when other forms of feedback, such as vision, are absent. They may also be important for balance.
9. Spinal circuits provide the neurological basis for perceptual–motor communication in the peripheral motor system. The simplest spinal circuit is the

reflex arc. Here a muscle contracts immediately in response to its own stretch.

10. According to one theory (servo theory), it was hypothesized that extrafusal contract via a stretch reflex triggered by the earlier activation of intrafusal. The timing of muscle-spindle discharge and extrafusal activity suggests, however, that intrafusal and extrafusal generally become active simultaneously. Such coactivation permits rapid correction for unexpected loads when movements are in progress.
11. Motor neurons not only activate muscles. They also excite Renshaw cells, which in turn inhibit the motor neurons themselves. This seemingly paradoxical effect has functional advantages. It provides a way of modulating the amount of input sufficient to activate motor neurons, and it increases the resolution of motor neuron activation.
12. Reciprocal inhibition exists between stretch receptors from one muscle and motor neurons for opposing muscles. Reciprocal inhibition prevents muscles from working against each other during response to muscle stretch.
13. The cerebellum regulates muscle tone, coordination, timing, and learning. If the cerebellum is disconnected from the spinal cord, muscle tone is adversely affected. Coordination deficits following cerebellar damage take the form of poor balance (*ataxia*), slurred speech (*dysarthria*), reaching too far (*hypermetria*), and oscillation in conjunction with purposeful movements (*intention tremor*). The sequencing of repetitive movements becomes difficult and requires more attention than usual. Timing difficulties associated with cerebellar damage take the form of abnormal durations and phase relations of EMG patterns as well as abnormal variability of rhythmic tapping behavior. The cerebellum's role in learning is suggested by the inability of animals with cerebellar damage to adapt eye–head coordination after wearing reversing prisms, by changes in cerebellar activity related to the development of limb coordination, and by the need for the cerebellum in learning visuo-motor anticipation.
14. The roles of the basal ganglia in motor control are suggested by behavioral consequences of basal ganglia disease. In Huntington's chorea, patients make wild, uncontrollable movements. In Parkinson's disease, patients exhibit shuffling gait, shaking motion at rest (*resting tremor*), slow movement initiation (*akinesia*), slow movement execution (*bradykinesia*), and muscle rigidity. The basal ganglia appear to play a role in initiating movements, modulating the global scale of movements, and regulating perceptual–motor interactions.
15. Localized electrical stimulation of the motor cortex elicits muscle twitches. The muscles that twitch depend on where the stimulation is applied. Varying the stimulation site allows investigators to develop “motor maps.” These are organized topographically, with neighboring regions representing neighboring musculature.

16. Cells of the motor cortex generally fire just before movements are made, especially before manual movements. The discharge of motor-cortex cells is related to the force and direction of movement. Different cells are tuned to different directions of movement, but individual cells respond to a range of directions. Outputs of the entire population of motor-cortex neurons lead to particular commanded directions (population coding).

17. Motor-cortex neurons receive sensory feedback from the muscles they drive, allowing for cortically mediated responses to muscle stretch. Because these responses have relatively long latencies, they are called long-loop reflexes. The immediate responses of motor-cortex neurons to muscle stretch are independent of volitional state, but later responses are influenced by expectancies.

18. The premotor cortex is primarily involved in readying postural muscles for forthcoming movements. It also plays a role in selecting movement trajectories.

19. The supplementary motor cortex is involved in the planning of extended movement sequences. Regardless of whether a person performs a finger sequence or imagines it, the supplementary motor cortex "lights up" in positron emission tomography (PET) scans of the brain.

20. The parietal cortex contains cells whose discharge properties are related to the behavioral relevance of spatial locations. In general, this brain region is crucial for spatially directed behavior. Damage to the parietal cortex can result in apraxia, an inability to perform purposeful motor acts when one's perceptual, cognitive, and motor faculties are otherwise intact. The incidence of apraxic symptoms in the left and right hand suggests that the memory representations for learned movement sequences are generally stored in the left hemisphere. The right hand receives motor commands directly from the left hemisphere, whereas the left hand receives motor commands from the right hemisphere after the right hemisphere has received signals from the left hemisphere via the corpus callosum.

21. Every motor act is the product of the collective activity of many brain centers. The brain centers discussed in this chapter are only some that contribute to motor control.

22. The study of motor physiology may provide insight into the physical sources of intentions. Thus far a single origination point for volitions has not been identified.

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PSYCHOLOGICAL FOUNDATIONS

■ INTRODUCTION

This chapter, in contrast to the last, presents a level of description somewhat removed from the physical basis of movement. The level of description is “psychological” in the sense that the structures and processes of interest are discussed without necessary reference to their physical realization. In physiology, by contrast, one is interested in functional relations among *physical* elements.

The chapter has three parts. The first is concerned with theories of serial order. Historically, the serial-order problem has been a focus of research for two main groups—psychologists working outside the field of motor control and researchers working on motor control not identified primarily as psychologists. This dual approach makes serial order an ideal starting point for the discussion.

The second part of the chapter is concerned with theories of skill learning. Again, this topic has been pursued by investigators both inside and outside the field of motor control. Diverse approaches have been taken to the skill-learning problem, and theorists have themselves become more and more adroit at explaining the facts of skill acquisition.

The third part of the chapter is concerned with topics related to the “information-processing” approach to performance. Some theoretical constructs from this framework have become controversial. Understanding the controversies provides useful background for the remaining chapters. It also gives a sense of the passion that many researchers have brought to bear in arguing for and against alternative approaches to motor control.

■ THEORIES OF SERIAL ORDER

Much of the work in psychology that bears on motor control has been concerned with the serial-order problem. Recall from Chapter 1 that the essence