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Fresco of dancing Peucetian women from the Tomb of the Dancers in the Corso Cotugno necropolis of Ruvo di Puglia, 4th–5th century BC. The tomb has a semichamber design. Its six painted panels depict 30 dancing women, moving from left to right with arms interlocked as though they were dancing in a circle around the interior of the tomb. The skeletal remains of the deceased in the tomb clearly belonged to a distinguished male warrior. The tomb is named after the dancing women that appear on the frescoes in the tomb. The panels with the frescoes are now exhibited in the Naples National Archaeological Museum, inv. 9353. (Source: https://en.wikipedia.org/wiki/Tomb_of_the_Dancers.)

V Movement

The capacity for movement, as many dictionaries remind us, is a defining feature of animal life. As Sherrington, who pioneered the study of the motor system pointed out, "to move things is all that mankind can do, for such the sole executant is muscle, whether in whispering a syllable or in felling a forest."*

The immense repertoire of motions that humans are capable of stems from the activity of some 640 skeletal muscles—all under the control of the central nervous system. After processing sensory information about the body and its surroundings, the motor centers of the brain and spinal cord issue neural commands that effect coordinated, purposeful movements.

The task of the motor systems is the reverse of the task of the sensory systems. Sensory processing generates an internal representation in the brain of the outside world or of the state of the body. Motor processing begins with an internal representation: the desired purpose of movement. Critically, however, this internal representation needs to be continuously updated by internally generated information (efference copy) and external sensory information to maintain accuracy as the movement unfolds.

Just as psychophysical analysis of sensory processing tells us about the capabilities and limitations of the sensory systems, psychophysical analyses of motor performance reveal the control rules used by the motor system.

Because many of the motor acts of daily life are unconscious, we are often unaware of their complexity. Simply standing upright, for example, requires continual adjustments of numerous postural muscles in response to the vestibular signals evoked by miniscule swaying. Walking, running, and other forms of locomotion involve the combined action of central pattern generators, gated sensory information, and descending commands, which together generate the complex patterns of alternating excitation and inhibition to the appropriate sets of muscles. Many actions, such as serving a tennis

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*Sherrington CS. 1979. 1924 Linacre lecture. In: JC Eccles, WC Gibson (eds). *Sherrington: His Life and Thought*, p. 59. New York: Springer-Verlag.

ball or executing an arpeggio on a piano, occur far too quickly to be shaped by sensory feedback. Instead, centers, such as the cerebellum, make use of predictive models that simulate the consequences of the outgoing commands and allow very short latency corrections. Motor learning provides one of the most fruitful subjects for studies of neural plasticity.

Motor systems are organized in a functional hierarchy, with each level concerned with a different decision. The highest and most abstract level, likely requiring the prefrontal cortex, deals with the purpose of a movement or series of motor actions. The next level, which is concerned with the formation of a motor plan, involves interactions between the posterior parietal and premotor areas of the cerebral cortex. The premotor cortex specifies the spatiotemporal characteristics of a movement based on sensory information from the posterior parietal cortex about the environment and about the position of the body in space. The lowest level of the hierarchy coordinates the spatiotemporal details of the muscle contractions needed to execute the planned movement. This coordination is executed by the primary motor cortex, brain stem, and spinal cord. This serial view has heuristic value, but evidence suggests that many of these processes can occur in parallel.

Some functions of the motor systems and their disturbance by disease have now been described at the level of the biochemistry of specific transmitter systems. In fact, the discovery that neurons in the basal ganglia of parkinsonian patients are deficient in dopamine was the first important clue that neurological disorders in the central nervous system can result from altered chemical transmission. Neurophysiological studies have provided information as to how such transmitters play a critical role in action selection and the reinforcement of successful movements.

Understanding the functional properties of the motor system is not only fundamental in its own right, but it is of further importance in helping us to understand disorders of this system and explore the possibilities for treatment and recovery. As would be expected for such a complex apparatus, the motor system is subject to various malfunctions. Disruptions at different levels in the motor hierarchy produce distinctive symptoms, including the movement-slowing characteristic of disorders of the basal ganglia, such as Parkinson disease, the incoordination seen with cerebellar disease, and the spasticity and weakness typical of spinal cord damage. For this reason, the neurological examination of a patient inevitably includes tests of reflexes, gait, and dexterity, all of which provide information about the status of the nervous system. In addition to pharmacological therapies, the treatment of motor system disorders has been augmented by two new approaches. First, focal stimulation of the basal ganglia has been shown to restore motility to certain patients with Parkinson disease; such deep-brain stimulation is also being tested in the context of other neurological and psychiatric conditions. And second, the motor systems have become a target for the application of neural prosthetics; neural signals are decoded and used to drive devices that aid patients with paralysis caused by spinal cord injury and stroke.

Part Editors: Daniel M. Wolpert and Thomas M. Jessell

Part V

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Principles of Sensorimotor Control

The preceding chapters in this book consider how the brain constructs internal representations of the world around us. These representations are behaviorally meaningful when used to guide movement. Thus, an important function of the sensory representations is to shape the actions of the motor systems. This chapter describes the principles that govern the neural control of movement using concepts derived from behavioral studies and computational models of the brain and musculoskeletal system.

We start by considering the challenges motor systems face in generating skillful actions. We then examine some of the neural mechanisms that have evolved to meet these challenges and produce smooth, accurate, and efficient movements. Finally, we see how motor learning improves our performance and allows us to adapt to new mechanical conditions, such as when using a tool, or to learn novel correspondences between sensory and motor events, such as when using a computer mouse to control a cursor. This chapter focuses on voluntary movement; reflexes and rhythmic movements are discussed in further detail in Chapters 32 and 33.

Voluntary movements are generated by neural circuits that span different levels of the sensory and motor hierarchies, including regions of the cerebral cortex, subcortical areas such as the basal ganglia and cerebellum, and the brain stem and spinal networks. These different structures have unique patterns of neural activity. Moreover, focal damage to different structures can cause distinct motor deficits. Although it is tempting to suggest that these individual structures have distinct functions, these brain and spinal areas normally work together as a network, such that damage to one component likely affects the function of all others. Many of the principles discussed in this chapter cannot be easily attributed to a single brain or spinal area. Instead, distributed neural processing is likely to underlie the computational mechanisms that subserve sensorimotor control.

The Control of Movement Poses Challenges for the Nervous System

Motor systems produce neural commands that act on the muscles, causing them to contract and generate movement. The ease with which we move, from tying our shoelaces to returning a tennis serve, masks the complexity of the control processes involved. Many factors inherent in sensorimotor control are responsible for this complexity, which becomes clearly evident when we try to build machines to perform human-like movement (Chapter 39). Although computers can now beat the world's best players at chess and Go, no robot can manipulate a chess piece with the dexterity of a 6-year-old child.

The act of returning a tennis serve illustrates why the control of movement is challenging for the brain (Figure 30–1). First, motor systems have to contend with different forms of uncertainty, such as our incomplete knowledge with regard to the state of the world and the rewards we might gain. On the sensory side, although the player may see the serve, she cannot be certain where her opponent will aim or where the ball might strike the racket. On the motor side, there is uncertainty as to the likely success of different possible returns. Skilled performance requires reducing uncertainty by anticipating events we may encounter (the trajectory of an opponent's tennis serve) and by motor planning (adopting an appropriate stance to return the expected serve).

Second, even if the player can reliably estimate the ball's trajectory, she must determine from sensory signals which of the 600 muscles she will use in order to move her body and racket to intercept the ball. Controlling such a system can be challenging as it is hard to explore all possible actions effectively in a system with many degrees of freedom (eg, a large number of individual muscles), making learning difficult. We will see how the motor system reduces the degrees of freedom of the musculoskeletal system by controlling groups of muscles, termed synergies, to simplify control.

Third, unwanted disturbances, termed noise, corrupt many signals and are present at all stages of sensorimotor control, from sensory processing, through planning, to the outputs of the motor system. For example, in a tennis serve, such noise will cause the ball to land in different places even when the server is trying to hit the same location on the court. Both sensory feedback, reflecting the ball's location, and motor outputs are contaminated with noise. The variability inherent in such noise limits our ability to perceive accurately and act precisely. The amount of noise in our motor commands tends to increase with stronger commands (ie, more force). This limits our ability to move rapidly and accurately at the same time and thus

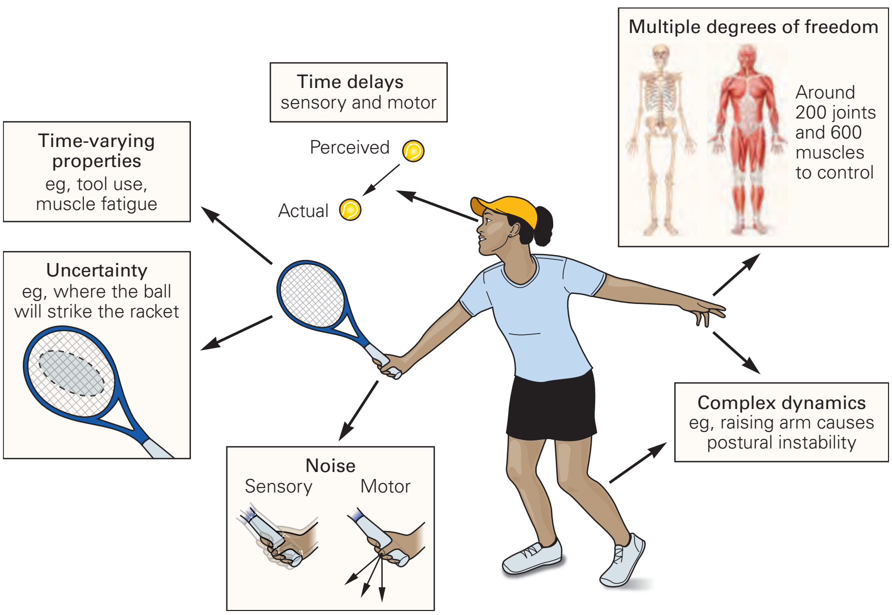

Figure 30–1 The challenges of sensorimotor control.

leads to a trade-off between speed and accuracy. We will see how efficient planning of movement can minimize the deleterious effects of noise on task success.

Fourth, time delays are present at all stages of the sensorimotor system, including the delays arising from receptor dynamics, conduction delays along nerve fibers and synapses, and delays in the contraction of muscles in response to motor commands. Together, these delays, which can be on the order of 100 ms, depend on the particular sensory modality (eg, longer for vision than proprioception) and complexity of processing (eg, longer for face recognition than motion perception). Therefore, we effectively live in the past, with the control system only having access to out-of-date information about the world and our own body. Such delays can result in instability when trying to make fast movements, as we try to correct for errors we perceive but that no longer exist. We will see how the brain makes predictions of the future states of the body and environment to reduce the negative consequences of such delays.

Fifth, the body and environment change both on a short and a long timescale. For example, within the relatively short period of a game, a player must correct for weakening muscles as she fatigues and changes in the court surface when it rains. On a longer timescale, the properties of our motor system change dramatically during growth as our limbs lengthen and increase in weight. As we will see, the ever-changing properties of the motor system place a premium on our ability to use motor learning to adapt control appropriately.

Finally, the relation between motor command and the ensuing action is highly complex. The motion of each body segment produces torques, and potentially motions, at all other body segments through mechanical interactions. For example, when a player raises the racket to hit the ball, she must anticipate destabilizing forces and counteract them to maintain balance. Indeed, when we raise our arms forward while standing, the first muscle to activate is an ankle flexor ensuring you remain upright. We will see how the sensorimotor system controls movement of different segments to maintain fine coordination of actions.

Actions Can Be Controlled Voluntarily, Rhythmically, or Reflexively

Although movements are often classified according to function—as eye movement, prehension (reach and grasp), posture, locomotion, breathing, and speech—many of these functions are subserved by overlapping groups of muscles. Moreover, the same groups of muscles can be controlled voluntarily, rhythmically, or reflexively. For example, the muscles that control respiration can be used to take a deep breath voluntarily before diving under water, to breathe automatically and rhythmically in a regular cycle of inspiration and expiration, or to act reflexively in response to a noxious stimulus in the throat, producing a cough.

Voluntary movements are those that are under conscious control. Rhythmic movements can also be controlled voluntarily but differ from voluntary movements in that their timing and spatial organization are to a larger extent controlled autonomously by spinal or brain stem circuitry. Reflexes are stereotyped responses to specific stimuli that are generated by neural circuits in the spinal cord or brain stem (although some reflexes involve pathways through cortex). These responses occur on a shorter timescale than voluntary responses.

Although we may consciously intend to perform a task or plan a certain sequence of actions, and at times are aware of deciding to move at a particular moment, movements generally seem to occur automatically. Conscious processes are not necessary for moment-to-moment control of movement. We carry out the most complicated movements without a thought to the actual joint motions or muscle contractions required. The tennis player does not consciously decide which muscles to use to return a serve with a backhand or which body parts must be moved to intercept the ball. In fact, thinking about each body movement before it takes place can disrupt the player's performance.

Motor Commands Arise Through a Hierarchy of Sensorimotor Processes

Although the final output to the musculoskeletal system is via motor neurons in the spinal cord, the motor control of muscles for a specific action occurs through a hierarchy of control centers. This arrangement can simplify control: Higher levels can plan more global goals, whereas lower levels are concerned with how these goals are implemented.

At the lowest level, muscles themselves have properties that can contribute to control even without any change in the motor command. Unlike the electric motors of a robot, muscles have substantial passive properties that depend on both the motor command acting on the muscle as well as the muscle's length and rate of change of length (Chapter 31). As a simple approximation, a muscle can be seen as acting like a spring (increasing tension as it is stretched and reducing tension as it is shortened) and damper (increasing tension as the rate of stretch increases). For small perturbations, these properties tend to act to stabilize the length of a muscle and hence stabilize the joint on which the muscle acts. For example, if an external perturbation extends a joint, the flexor muscles will be stretched, increasing their tension, while the extensor muscles will be shortened, reducing their tension, and the imbalance in tension will tend to bring the joint back toward its original position. A particular advantage of such control is that, unlike higher levels in the motor hierarchy, such changes in force act with minimal delay as they are simply an effect of passive physical properties of the muscles.

In addition to the passive properties of muscles, sensory inputs can cause motor output directly without the intervention of higher brain centers. Sensorimotor responses, such as spinal reflexes, control for local disturbance or noxious stimuli. Reflexes are stereotyped responses to specific stimuli that are generated by simple neural circuits in the spinal cord or brain stem. For example, a spinal flexor withdrawal reflex can remove your hand from a hot stove without any descending input from the brain. The advantage of such reflexes is that they are fast; the disadvantage is they are less flexible than voluntary control systems (Chapter 32). Again, there is a hierarchy of reflex circuits. The fastest is the monosynaptic stretch reflex, which drives contraction of a stretched muscle. In this reflex circuit, sensory neurons that are activated by stretch receptors in the muscle (the muscle spindle) directly synapse onto motor neurons that cause the same muscle to contract. The time from the stimulus to the response is around 25 ms. This reflex can be tested clinically by striking the quadriceps muscle tendon just below the patella.

While this monosynaptic stretch reflex is not adaptable on short timescales, multisynaptic reflexes, which involve higher level structures such as motor cortex, can produce responses at around 70 ms. Unlike the monosynaptic reflex, multisynaptic reflexes are adaptable to changes in behavioral goals because the circuit connecting sensory and motor neurons can be modified by task-dependent properties. The strength of a reflex tends to increase with the tension in a muscle (called gain-scaling), and therefore, reflexes can be amplified by co-contracting the set of muscles around a joint so as to respond to perturbations with a greater force. In fact, we use such co-contraction when holding the hand of a rebellious child when crossing a road. Such a strategy can amplify the reflexes, thereby reducing deviations of the arm caused by random external forces.

Finally, voluntary movements are those that are under conscious control by the brain. Voluntary movements can be generated in the absence of a stimulus or used to compensate for a perturbation. The time to generate a voluntary movement in response to a physical perturbation depends both on the nature of the perturbation (modality and size) as well as whether the response can be specified before the perturbation occurs. For example, a voluntary correction to a small physical perturbation can occur with a latency of about 110 ms.

Although we have described clear distinctions between the different levels of the motor hierarchy, from reflexes through to voluntary control, in reality, such distinctions are blurred in a continuum of responses spanning different latencies. Increasing the response time permits additional neural circuitry to be involved in the sensorimotor loop and tends to increase the sophistication and adaptability of the response, leading to a trade-off between the speed of the response and the sophistication of processing as one ascends the motor hierarchy.

Motor Signals Are Subject to Feedforward and Feedback Control

In this section, we will first illustrate some principles of control that are important for dealing with the problem of sensory delays, sensory noise, and motor noise. For simplicity, we confine our discussion to relatively simple movements, such as moving the eyes in response to head movements or moving the hand from one location to another. We consider two broad classes of control, feedforward and feedback, which differ in their reliance on sensory feedback during the movement.

Feedforward Control Is Required for Rapid Movements

Some movements are executed without monitoring the sensory feedback that arises from the action. In such feedforward control situations, the motor command is generated without regard to the sensory consequences. Such commands are therefore also termed *open-loop*, reflecting the fact that the sensorimotor loop is not completed by sensory feedback (Figure 30–2A).

Open-loop control requires some information about the body so that the appropriate command can be generated. For example, it should include information about the dynamics of the motor system. Here, "dynamics" refers to the relation between the motor command (or the torques or forces) applied and the ensuing motion of the body, for example, joint rotations. For perfect open-loop control, one needs to