
Control of Movement

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The Neural Control of Movement

The Spectrum of Movements
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Neural Structures Involved in Movement

Movement is crucial to the survival of all organisms. Even unicellular organisms such as *Escherichia coli* can move toward those chemicals critical for their metabolism (see Chap. 5). More complicated creatures such as coelenterates move only slowly but require motile tissues to attract and capture passing prey. Birds are not only capable of the incredible motor feat of flying but also rely on posturing and movement to attract a mate. Mammals are endowed with probably the greatest repertoire of motor behaviors. These range from the motility of the gut and the beating of the heart to the fine finger movements of an accomplished pianist. All these movements perform quite different functions, so it is not surprising that they are accomplished in different ways.

THE SPECTRUM OF MOVEMENTS

We are all aware that some movements seem to occur automatically, whereas others require effort and concentration. The simplest movement is the rapid response to a noxious sensory stimulus.

Such movements occur after a very short latency (<50 ms) and have a stereotyped trajectory. Examples include withdrawing your hand from a hot stove or lifting your foot from a tack. Because they are stereotyped and rapid (and therefore probably are controlled by relatively few neurons; Chap 24), these motor acts have been called *reflexes*. Reflexes usually are not under voluntary control, so that when the stimulus specific for the reflex occurs *unexpectedly*, the reflex movement is elicited automatically and cannot be modified. Indeed, many reflexes can be elicited in unconscious individuals or those in whom the cerebral cortex has been destroyed. Under special conditions, however, many reflexes can be modified and even prevented from occurring. For example, blinking, sneezing, and even withdrawing from a noxious stimulus (certainly if one is a fakir) can be suppressed with intense voluntary effort. However, some reflexes, such as the constriction of the pupils to a sudden bright light, are difficult if not impossible to influence by voluntary effort.

At the other end of the spectrum are movements that are completely under voluntary control. For volitional movements, such as painting, one can choose the direction, extent, trajectory, and timing of the movement. Furthermore, voluntary movements can be modified while they are occurring. In contrast with reflexes, voluntary movements are rarely triggered by any obvious sensory stimulus and are typically executed over longer periods of time. Furthermore, they may be affected by

such esoteric factors as attention and motivation and therefore may be under the influence of many neuronal structures scattered throughout the central nervous system. Most voluntary movements must be learned and require practice to become perfect. Once learned, a complicated motor behavior is apparently stored as a package called a *motor program* that can be called up whenever it is required. For example, one does not consciously control each part of the sequence of movements required to sign one's name, and an accomplished typist no longer thinks about the details of his finger placements.

A class of movements that lie intermediate to reflexes and completely voluntary movements are those involved in rhythmic behaviors such as breathing, chewing, and walking. These movements can be initiated and terminated voluntarily but, once initiated, they proceed automatically and are characterized by a repeated sequence or pattern of movements. As we shall see later (Chap. 26), rhythmic movements are controlled by neural networks in the spinal cord or brain stem that feature reciprocal connections between pools of neurons generating opposite behaviors (e.g., inspiration and expiration). These neural networks, called *pattern generators*, may be set in motion (or "triggered") by a sensory or a command signal. Once underway, most rhythmic behaviors can also be influenced by sensory stimuli. For example, the pattern of chewing is modified to compensate for the different textures of food.

Movements can therefore be considered to range from essentially automatic (the reflex) through semiautomatic to completely volitional. The nervous system controls these different movements in different ways according to their purpose. For example, the leg movements used in locomotion may be optimized for speed, whereas the delicate hand and finger movements of a watchmaker may require an exquisite control of position. We now consider the movement parameters that *could* be controlled so that we can better appreciate how motor systems are designed and can better interpret the various signals that are carried in the discharge of single neurons involved with movement.

WHAT IS CONTROLLED DURING MOVEMENT?⁷

Movement is produced by the contraction and relaxation of muscles. These muscular changes create forces that act on the load imposed by a body part (e.g., a limb) and any external object

that must be moved. The parameters of the resulting movement (i.e., displacement [or position], velocity, and acceleration) are then determined according to the laws of mechanics.

The nervous system must apply neural signals that are appropriate to control the desired parameter. In some situations, the controlled parameter may be force (e.g., the delicate isometric contraction required to hold a fragile glass). In others, it may be position (e.g., the finger placements of a typist on a computer keyboard), or velocity, or acceleration. Alternatively, the controlled variable may involve a pair of movement parameters. For example, stiffness, which is the ratio of force to displacement, has been proposed as the controlled parameter in some limb movements.²

In addition to the control of these obvious movement parameters, other control strategies have been proposed. For example, control system theory, especially as applied to the field of robotics, has suggested that some movements may minimize the energy consumed, the time taken, or the variation of the movement about a given trajectory.¹

These examples illustrate that different movements can be accomplished by controlling a wide variety of parameters. Furthermore, different control strategies can be exerted on the same muscle, according to how it is used. For example, the control of the jaw muscles during speaking is quite different from that during chewing, especially when one encounters foods with different textures (e.g., a raw carrot vs. mashed potatoes). Similarly, the control of the hand when performing a powerful grip is different from that required when writing.

Another example is the control of the joint angle between two parts of a limb. Muscles act reciprocally to produce movement in opposite directions around a joint. For example, flexion of the elbow (Fig. 22-1) is produced by contraction of the biceps and relaxation of the triceps, whereas extension of the elbow requires just the opposite pattern of muscle action. An entirely different pattern of neural signals, however, is required to co-contrast both sets of muscles to stabilize the joint against movement in either direction. Joint angle may be established by controlling yet another movement parameter, muscle length. Since muscles are elastic, they exhibit the properties of springs. To produce different forearm positions, therefore, the neural signals could set the length of the opposing muscles, thereby producing, according to Hooke's law, the forces required to establish the correct joint angle.

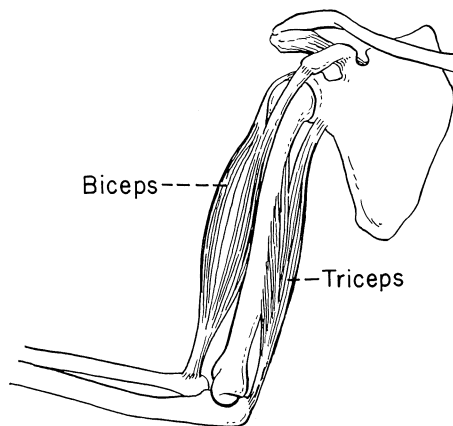


Figure 22-1 Schematic representation of the pair of antagonistic muscles (biceps and triceps) that bend the elbow.

HOW ARE MOVEMENTS CONTROLLED?^{3, 5}

The control of movement is accomplished by signals generated in the central nervous system. Figure 22-2 shows the most simple scheme for the neural control of the angle of a limb joint. Movement is produced by muscular contractions con-

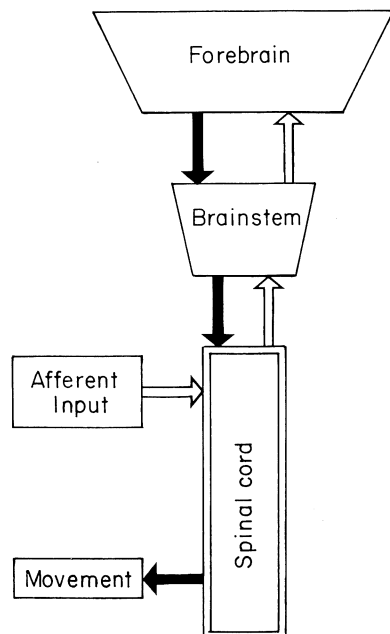


Figure 22-2 A simple schematic diagram illustrating the participants in the neural control of movement. Motor signals follow the solid arrows and sensory signals follow the open arrows. (After Wetzel, M.C.; Stuart, D.G. In *Mechanics and Energetics of Animal Locomotion*, 115-152. London, Chapman & Hall, 1977.)

trolled by a motor signal generated in the spinal cord. This spinal motor signal results from the integration of afferent signals from the limb (and other parts of the body) with motor command signals that descend from supraspinal brain structures such as the brain stem and forebrain. The descending supraspinal command signal is based, in part, on the same afferent information that influences the spinal cord directly.

In order to execute an accurate voluntary limb movement, the central nervous system takes advantage of afferent signals that reach it at many different levels. At the first level, a movement can be influenced by local cues generated in the limb that is moved. These local cues (e.g., tactile signals or signals about the state of the limb's muscles) converge with descending motor command signals onto common neuronal elements in the spinal cord to create the spinal motor signal. This interaction is schematized by the local feedback circuit shown in Figure 22-3A. At a second level, the same afferent information is delivered to the brain (Fig. 22-3A, central feedback), where it can influence the descending signal. Finally, the movement of the limb also is monitored by watching it. This third level can use afferent information from vision as well as a variety of other sensory modalities that are not shared with spinal interneurons.

Although all three levels usually act together, they can be thought of as parts of a hierarchy involved in the control of movement. Local feedback, the lowest level of the hierarchy, can have the most immediate influence upon the movement, but the raw afferent signals may not be sufficiently integrated with other afferent signals to provide anything more than a rather gross movement. Central feedback, the second level of the hierarchy, allows not only the convergence of various afferent signals but also interactions with voluntary command signals. Because this processing takes time, however, the influence of central feedback on the descending command signal is delayed. Finally, the feedback provided by other afferent modalities takes longer still, since it requires the most processing. These other afferent signals, however, may provide the most accurate control. For example, local and central feedback might allow one eventually to thread a needle or hit a nail with a hammer, but both tasks are greatly facilitated if the eyes are open.

The use of feedback provides a means by which an actual movement (or afferent signals describing the movement) can be compared with a command signal for the desired movement. The diagram of Figure 22-3A has three feedback loops. A system

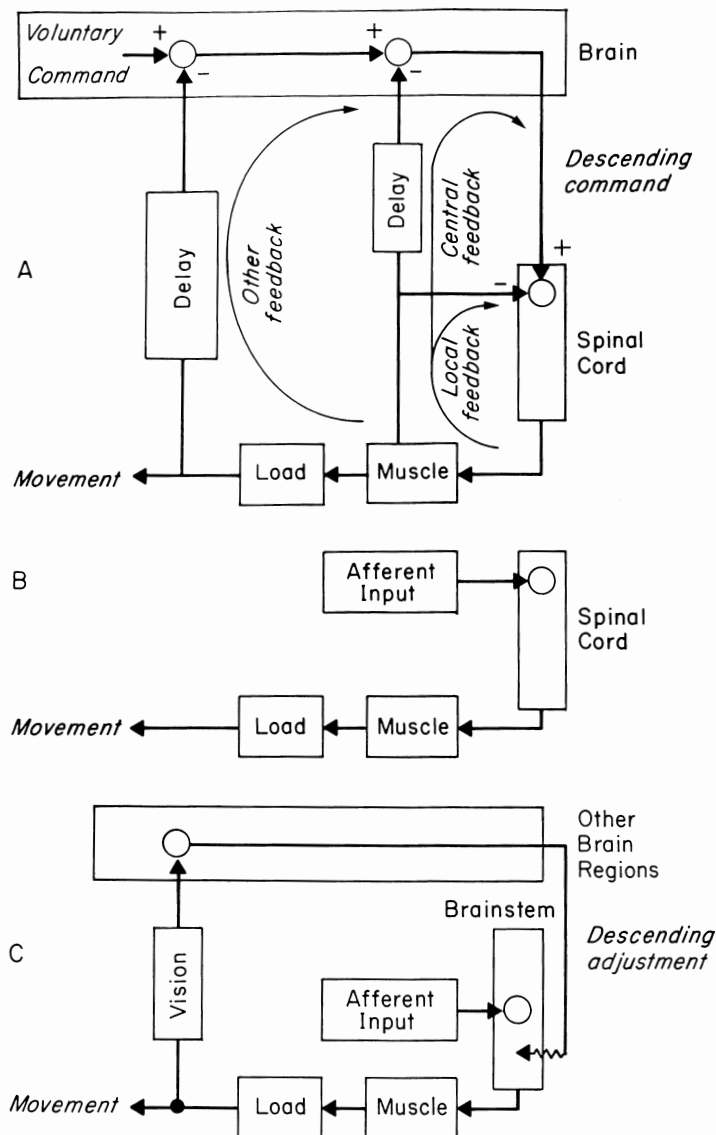


Figure 22-3 Schematic diagrams illustrating different strategies for the control of movement. *A*, A feedback system with both a local pathway and two longer pathways with delays. *B*, An open loop system with no feedback control. *C*, An open loop system in the brain stem whose elements are maintained in calibration by parametric control from other brain regions (see text for further explanation).

that uses such a control strategy is called a “closed loop” system.

Feedback generally improves the accuracy of a movement but delays, and possibly slows, its execution. Indeed, the brain often initiates and controls movement on the basis of sensory information that is distinctly out of date. In situations in which speed is paramount but the trajectory and accuracy of a movement are not, the nervous system eschews the feedback comparison of the actual with the desired movement. Instead, an afferent input always elicits a movement that can't be controlled. Such an “open-loop” system is depicted in Figure 22-3B. Some reflex-evoked

movements, especially those triggered by noxious stimuli, can be considered to operate open loop.

Some reflexes, such as the vestibulo-ocular reflex (or VOR), however, are both fast *and* relatively accurate. If the head is turned suddenly, the VOR produces compensatory eye movements that minimize the slip of the visual world across the retina. Since the VOR produces these eye movements within 10 ms of the onset of head rotation, it is too fast to afford negative feedback and thus operates open loop. Nevertheless, the accuracy of the VOR must be maintained even if its neuronal elements are affected by disease and aging. An accurate VOR is maintained by a strategy called *parametric control*. Since an inappropriately adjusted VOR causes the visual

world to slip across the retina during head rotation, the visual system monitors the amount of slip and adjusts the brain stem elements (or parameters) to eliminate it (Fig. 22-3C). Parametric control allows the VOR to be protected against gradual changes in its individual elements without the use of feedback control, thereby allowing the VOR to retain its rapid response (Chap. 27 gives further details).

For rapid voluntary movements, the delays inherent in feedback control can be overcome by computing the descending command signal in advance with as much accuracy as possible. Such *preprogramming* is a particularly effective strategy if the body part to be moved usually encounters a constant load, as in the rapid movements of the eyes and head. Preprogramming may also be effective when large limb movements are executed against predictable loads. Figure 22-4 shows 20° flexions of the wrist (upper record) against a spring load in a patient with a sensory neuropathy that has destroyed all of his large sensory fibers (i.e., those that transmit information about touch and

the state of muscles, such as length. Even when blindfolded to remove the last remaining afferent signal about the movement, the patient made remarkably accurate initial movements to the desired position (Fig. 22-4, middle trace). When he tried to *hold* his wrist in its new position, however, he was generally unable to do so. In this patient, therefore, the motor signals for the dynamic phase of the movement appear to be preprogrammed, whereas the holding (or static) phase depends upon afferent feedback.

In addition to participating in movement, descending motor signals may also impinge upon sensory relay nuclei (e.g., in the brain stem) where they can affect the transmission of afferent information. Such a *corollary discharge* might impinge on neurons that relay afferent information, thereby providing a signal that helps them to distinguish sensory signals induced by external stimuli per se from those induced as a consequence of the movement. Corollary discharges may also contribute to the perception of muscular force or effort and may thus participate in sensations of heaviness.⁴ Finally, corollary motor command signals can be used to construct an internal neural replica (or *efference copy*) of an impending movement. Such a neural copy of the movement would provide an important control signal in those motor systems in which the somatosensory feedback from muscles is inadequate (e.g., the system that controls the position of the eye).

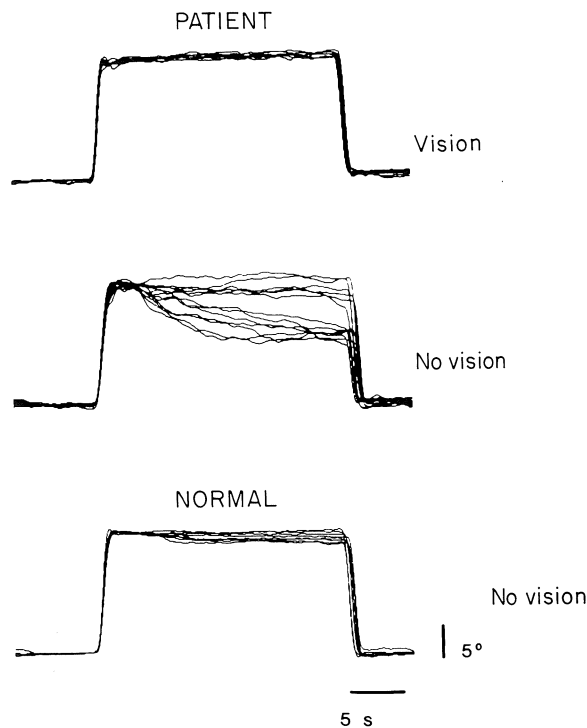


Figure 22-4 Flexion and extensions of the wrist against an elastic load by a patient with a large-fiber sensory neuropathy and by a normal subject. These movements have a dynamic phase that flexes the wrist angle through 20° and a "hold" phase that keeps the wrist in its flexed position. The hold phase of movement made without vision is significantly impaired in the patient but only modestly affected in the normal subject. (After Sanes, J.N., et al. *Human Neurobiol.* 4:101-114, 1985.)

NEURAL STRUCTURES INVOLVED IN MOVEMENT

Neural structures can be considered to deal with movement if they are involved in producing one of the various motor signals or processing the sensory signals required for accurate control. Four different experimental approaches have been used to implicate a brain structure in the control of movement. First, natural or experimentally produced lesions of a neural structure involved in movement are expected to produce deficits in some aspect of movement. Such deficits might range from a complete paralysis to an inability to suppress wild, involuntary movements (ballismus). Lesions of some structures may only affect the ability to make subtle modifications in a normal movement. Second, electrical stimulation of some putative motor structures can be expected either to produce an overt movement or to affect a movement that is in progress. Of course, the more the central nervous system is depressed by anesthesia or the further the structure is removed from the muscle involved, the less likely is its stimulation to produce an overt movement. Third, by

recording from neurons in awake, moving animals, structures can be identified whose neuronal firing patterns are related to one or more of the movement parameters discussed above. As may be recalled from the discussion of corollary discharge, such neurons may or may not actually participate in motor control. Finally, anatomical techniques can be used to identify structures connected to those areas that have been identified by lesion, stimulation, and recording studies as being involved with movement. One or more of these types of evidence implicate several major subdivisions of the nervous system in the generation of movement; these regions and their interconnections are indicated schematically in Figure 22-5.

The most crucial part of the motor system is the *muscle* and its efferent neural element, the *motoneuron*, without which force could not be generated. Lesions of motoneurons produce a complete paralysis of movement, and suprathreshold electrical stimulation of the normal, intact motor nerve or its muscle invariably evokes muscle contraction. Sensory signals from the muscle and its body part

(i.e., the periphery) enter the *spinal cord* over sensory afferents, which may influence motoneurons directly or via only an additional interneuron or two. Through such "simple" circuits, restricted to the periphery and the spinal cord, stimuli that evoke reflexes can produce appropriate responses in motoneurons. The isolated spinal cord can mediate many reflexes, such as withdrawal from a noxious stimulus or the knee jerk, elicited by striking the patellar tendon below the knee. These *segmental* circuits, which provide rapid responses with minimal delays, are important for protective reflexes that do not require elaborate processing of afferent data. Furthermore, the spinal cord alone also is capable of generating the neural patterns required for many coordinated limb movements, such as those that stabilize three of a quadruped's limbs when the fourth is withdrawn or those that produce the crude sequential movements of the four limbs during locomotion (Chap. 26).

Motoneurons can be influenced not only by local signals originating in peripheral structures but also

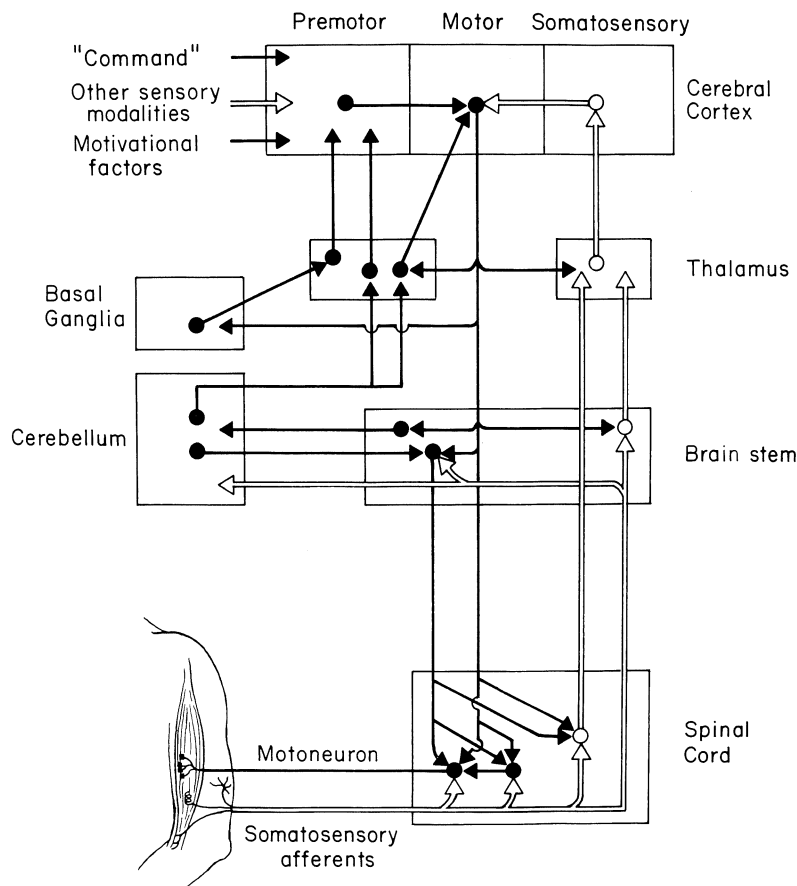


Figure 22-5 Major central nervous system structures and pathways involved in the neural control of movement. Open arrows trace sensory signals; solid arrows represent either motor or combined sensory and motor pathways.

by signals descending from the *brain stem* (Fig. 22–5). The large majority of these descending influences are mediated by the same spinal interneurons that are involved in spinal segmental reflexes (Chap. 26). Indeed, the descending signals must be tailored to make appropriate interactions with the current state of the reflex circuitry. Descending signals from the brain stem are issued from a variety of nuclei, including many that lie in a core of gray matter called the *reticular formation*, which runs the length of the brain stem from the mesencephalon to the medulla. Many of the brain stem nuclei in turn receive movement-related signals from the *sensorimotor cortex*. Even in the absence of inputs from these higher centers, however, the brain stem adds to the capabilities of the isolated spinal cord. For example, a decerebrate animal whose neuraxis has been transected at the level of the midbrain is able to right itself and make some postural adjustments. The sensory signals for these compensatory behaviors originate in the vestibular apparatus (not shown) and act through circuitry confined to the medullary brain stem. The compensatory eye movements generated by vestibular stimuli also appear to be normal. In addition, rhythmic motor behaviors such as respiration and mastication, which have their origins in the medullary and pontine reticular formations, respectively, are also intact.

The *sensorimotor cortex* plays a crucial role in generating those voluntary movements that are fashioned by both sensory input and motivational set (Chap. 28). Sensory input reaches the cortex via pathways involving the brain stem and *thalamus*. The relay in the brain stem also allows the afferent signals to influence descending motor signals (Fig. 22–5). Although most of the descending cortical signals affect the spinal cord indirectly through relays in the brain stem, some travel all the way to the spinal cord (the corticospinal system), where a few even influence motoneurons directly.

Finally, there are two movement-related structures that, because of their connections, seem strategically situated to shape motor behavior. Both the *basal ganglia* and *cerebellum* send prominent projections to the thalamus and thence to

premotor and motor areas of the cerebral cortex. Both also receive major inputs from these and other cortical areas. Whereas the basal ganglia receive little, if any, direct sensory input to shape their activity, the cerebellum receives strong, short-latency sensory inputs from virtually every somatosensory receptor, as well as from the visual, vestibular, and auditory modalities. Although neither the basal ganglia (Chap. 30) nor the cerebellum (Chap. 29) is necessary for the production of *any* movement, they are both essential for postural adjustments and for ensuring that coordinated movements are smooth and accurate. The cerebellum may also be involved in the acquisition of new motor behaviors (Chap. 27).

The following chapters consider, in detail, the role of each of these structures in the generation of movement. As seen from Figure 22–5, however, all of the areas involved with movement have extensive reciprocal connections, making it impossible to attribute specific motor functions to individual structures. Nevertheless, the combined evidence from electrophysiological, anatomical, and clinical studies has led to some broad principles of motor organization that are discussed in this section on movement.

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