Figure 30–13 Learning new coordination patterns in walking.

A. A subject walks on a split-belt treadmill. When the two belts move at the same speed, subjects have a symmetric gait pattern with equal step lengths.

B. In an adaptation study, the speeds of the belts are initially the same, then become split so that the right belt moves faster than the left, and then finally return to the same speed (**top**). Step length symmetry is initially lost when the belts move at different speeds, causing the subject to limp. Over time, the symmetry is restored and the limping is abolished. When the belts are once again moving at the same speed, an aftereffect is seen (**middle**).

Maurice Smith and colleagues have shown that this type of adaptation is composed of multiple underlying processes that adapt on different timescales (**bottom**). The change in the step length symmetry is composed of two processes: a fast process (**light green line**) that adapts quickly but also rapidly forgets what has been learned, and a slow process (**dark green line**) that learns more slowly but has better retention. These processes both adapt to learn from the error, and the sum of these processes is the final adaptation (**blue line**). This dual-rate learning system gives rise to the typical double exponential learning curves seen in many forms of adaptation in which adaptation is initially fast but tends to slow down as learning proceeds. (Adapted, with permission, from Roemmich, Long, and Bastian 2016.)

that shift visual space, for example, they initially miss when reaching to targets but soon learn to reach correctly. After repeated trials, the mere feel of the glasses, without the prisms in place, is sufficient to evoke the adaptive behavior appropriate for the prisms.

In general, we can quantify performance with two measurements, accuracy and precision. Accuracy is a measure of systematic errors or biases, for example, on average how far a series of thrown darts are away from the target. In contrast, precision is a measure of random errors, or statistical variability, in our actions. Both accuracy and precision contribute to performance. In general, accuracy can be improved by adapting or calibrating motor commands so as to reduce systematic errors. Although there is always some variability in movement arising from irreducible sensory and motor noise, the variability, as we have seen, can be reduced through planning so as to have minimal impact on task success. Most motor learning tends to become automatic (ie, implicit) with time, but early learning of some tasks can be aided by explicit learning (ie, strategy), such as a verbal instruction on how best to approach the task.

Not all sensory modalities are equally important in learning all motor tasks. In learning dynamic tasks, proprioception and tactile input are more important than vision. We normally learn dynamic tasks equally well with or without vision. However, individuals who have lost proprioception and tactile input have particular difficulty controlling the dynamic properties of their limbs or learning new dynamic tasks without vision (Box 30–3).

Skill Learning Relies on Multiple Processes for Success

In contrast to error-based learning in which the sensorimotor system adapts to a perturbation to return to pre-perturbation performance, learning skills such as tying one's shoelaces, juggling, typing, or playing the piano instead involves improving performance in the absence of a perturbation. Such learning tends to improve the speed–accuracy trade-off. Initially, we may be able to hit the correct keys on a keyboard when paced 1 second apart, but with practice, the same accuracy can be achieved at an increasingly quickening pace.

Box 30–3 Proprioception and Tactile Sense Are Critical for Sensorimotor Control

While visual impairment certainly has limiting effects on sensorimotor control, blind people are able to walk normally and reach and grasp known objects with ease. This is in stark contrast to the rare loss of proprioceptive and tactile sense.

Some sensory neuropathies selectively damage the large-diameter sensory fibers in peripheral nerves and dorsal roots that carry most proprioceptive information. Impairments in motor control resulting from loss of proprioception have fascinated neurologists and physiologists for well over a century. Studies of patients with sensory neuropathies provide invaluable insight into the interactions between sensation and movement planning.

As expected, such patients lose joint position sense, vibration sense, and fine tactile discrimination (as well as tendon reflexes), but both pain and temperature senses are fully preserved. Patients with peripheral neuropathies are unable to maintain a steady posture, for example, while holding a cup or standing, with the eyes closed. Movements also become clumsy, uncoordinated, and inaccurate.

Some recovery of function may occur over many months as the patient learns to use vision as a substitute for proprioception, but this compensation still leaves patients completely incapacitated in the dark. Some of this difficulty reflects an inability to detect errors that develop during unseen movements, as occurs if the weight of an object differs from expectation.

Peripheral neuropathies are particularly incapacitating when patients try to make movements with rapid direction reversals. Analyses of the joint torques during these movements show that subjects with intact proprioception anticipate intersegmental torques, whereas those without proprioception fail to do so (Figure 30–14).

However, the same patients easily adapt to drastic kinematic changes, such as tracing a drawing while viewing their hand in a mirror. In fact, they perform better than normal subjects, perhaps because they have learned to guide their movements visually and, because they lack proprioception, do not experience any conflict between vision and proprioception.

Even in normal subjects, the relative importance of tactile input in manipulation tasks can be easily demonstrated. It is relatively easy to light a match with one's eyes closed. However, if the tips of the digits are made numb with local anesthetic, then even under full vision the task is remarkably hard because the match tends to slip from the fingers.
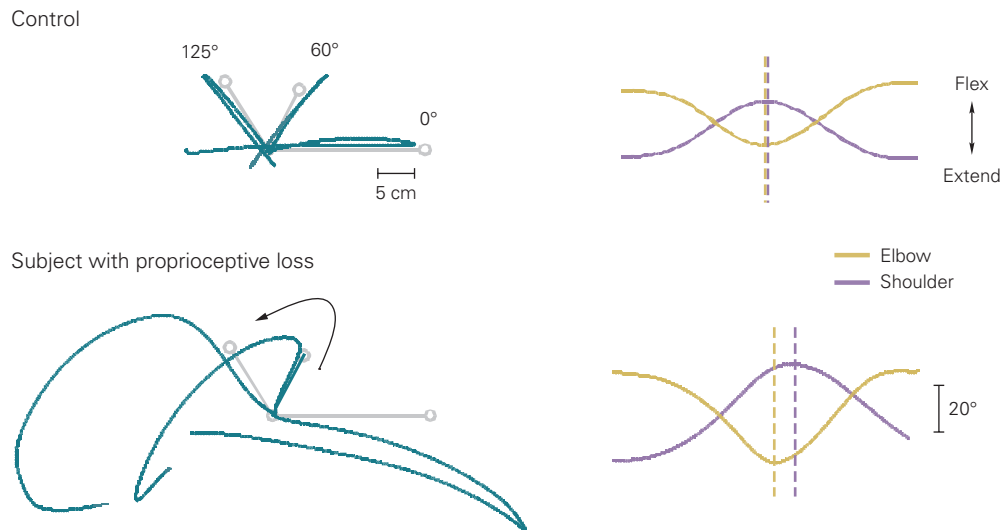
Figure 30–14 Patients lacking proprioception cannot make an accurate movement that requires a rapid reversal in path. (*Left*) The subject tries to trace a template (**gray line**) while her hand is hidden from view. The joint angles for the elbow and shoulder of a normal subject show good alignment (*Right top*), leading to an accurate reversal (*Left top*). In contrast, the timing of the joint reversal is poor in subjects who lack proprioceptive input (*Right bottom*), leading to large errors in the path (*Left bottom*). These patients cannot anticipate and correct for the intersegmental dynamics that occur around the path reversal. (Adapted, with permission, from Sainburg et al. 1995.)

For some skills, there can be a complex relation between the actions performed and success or failure at the task. For example, when children first sit on a swing, they have to learn the complex sequence of leg and body movements required to make the swing go higher. In contrast to error-based learning, there is no readily available error signal that can be used to adjust the current action because the swing's height is not directly determined by the current action but by a long history of body and leg motion. Learning in such complex scenarios can be achieved using reinforcement learning in which the sensorimotor system adjusts its commands in an effort to maximize reward, that is, task success. In the most general form, the performance measure that the reinforcement learning tries to maximize is the sum of all future rewards. However, as we tend to favor an immediate versus time-delayed reward, the sum is typically weighted to reflect this by progressively discounting future rewards.

Reinforcement learning is more general than error-based learning in that the training signal is success or failure, rather than an error at each point in time. Another distinguishing property of reinforcement learning is that the success or failure that the learning system receives can depend in nontrivial ways on the history of the actions taken. For tasks that require a complex sequence of actions to take place to achieve a goal, such as tying one's shoelaces, and the outcome or reward is removed in time from the action, error-based learning cannot easily be applied. A key problem that reinforcement solves is that of credit assignment: Which action within a sequence should we credit or blame when we eventually succeed or fail? This is just the sort of problem reinforcement learning algorithms are good at solving.

There are two main classes of reinforcement learning, those that depend on an internal model and those that do not. Model-based reinforcement builds a model of the task (eg, the structure of a maze). With such a model, the learner can efficiently plan in a goal-directed manner. In contrast, with model-free reinforcement learning, the learner simply associates movements with success or failure; those that lead to success are more likely to be performed again. Such learning can lead to motor habits. While model-free learning avoids the computational burden of building a model, it is also less able to generalize to novel situations. These two types of reinforcement learning can even act together, and different tasks can rely on them to different extents. Dopaminergic systems in the basal ganglia have been tied to signals that one would expect in reinforcement learning, such as expected reward. Moreover, dysfunction in these systems is related to movement disorders, addiction, and other problems that could be related to reinforcement signals (Chapter 38).

Finally, the development of efficient strategies plays a key part in motor skill acquisition. Skill learning for real-world tasks typically involves a sequence of decision-making processes at different spatiotemporal scales. The skill of a tennis player, for example, is not only determined by the precision with which she can strike the ball but also by the speed with which she can make the correct decision on where to aim it and how well she uses her senses to extract task-relevant information.

Sensorimotor Representations Constrain Learning

The information obtained during a single movement is often too sparse or noisy to unambiguously determine the source of error. For example, if a tennis player hits a shot into the net on the serve, the problem could be that the ball was not thrown high enough, the ball was hit too early, the racquet strings are loose, there was a gust of wind, or the player is fatigued. If the racquet dynamics have changed, the player would do well to adapt to these for the next shot. If a temporary gust of wind was the problem, then no adjustment is needed. To resolve this issue, the sensorimotor learning system constrains the way in which the system is updated in response to errors. These constraints reflect the internal assumptions about the task structure and the source of errors and determine how the system represents the task. Indeed, on a slower timescale, learning itself can alter the representation.

While the final output of the motor system is the contraction of its 600 or so muscles, it is not the case that the brain controls each independently. In current models of sensorimotor control, motor commands are generated by multiple modules that can be selectively engaged depending on the requirements of the task. Examples of modular architectures include multiple internal models, motor primitives, and motor synergies (Chapter 36).

Motor primitives can be thought of as neural control modules that can be flexibly combined to generate a large repertoire of behaviors. A primitive might represent the temporal profile of a particular muscle activity or a set of muscles that are activated together, termed a synergy. The overall motor output will be the sum of all primitives, weighted by the level of the activation of each module. The makeup of the population of such primitives then determines which structural constraints are imposed on learning. For example, a behavior for which the motor system has many primitives will be easy to learn, whereas a behavior that cannot be approximated by any existing primitives would be impossible to learn.

Highlights

1. The primary purpose of the elaborate information processing and storage that occurs in the brain is to enable us to interact with our environment through our motor system.
2. Our infinitely varied and purposeful motor behaviors are governed by the integrated actions of the motor systems, including the motor cortex, spinal cord, cerebellum, and basal ganglia.
3. To control action, the central nervous system uses a hierarchy of sensorimotor transformations that convert incoming sensory information into motor outputs.
4. There is a trade-off in the speed versus sophistication of the different levels of sensorimotor response from rapid reflexes to slower voluntary control.
5. The motor systems generate commands using feedforward circuits or error-correcting feedback circuits; most movement involves both types of control.
6. The brain uses internal models of the sensorimotor system to facilitate control.
7. The state of the body is estimated using both sensory and motor signals together with a forward predictive mode to reduce the adverse effects of delays in feedback.
8. Variability in the sensory inputs and motor outputs together with inaccuracies in sensorimotor transformations underlie the errors and variability in movement, leading to the trade-off between speed and accuracy.
9. Motor planning can use the redundancy of the motor system to move in such a way as to reduce the negative consequences of motor noise while reducing effort.
10. Motor control circuits are not static but undergo continual modification and recalibration throughout life.
11. Motor learning improves motor control in novel situations, and different forms of sensory information are vital for learning. Error-based learning is particularly important for adapting to simple sensorimotor perturbations. Reinforcement learning is particularly important for more complex skill learning and can rely on a model (model-based) or on simply reinforcing motor actions directly (model-free).
12. The motor representations used by the brain constrain the way the sensorimotor system updates during learning.
13. Studies of sensorimotor control have focused on developing a detailed understanding of relatively simple tasks, such as reaching and walking. Although these tasks are amenable to analysis and modeling, they do not capture the full complexity of real-world motor control. The challenge will be to determine if these principles can be generalized to tasks such as tying shoelaces and learning to skateboard.

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31

The Motor Unit and Muscle Action

ANY ACTION—ASCENDING A FLIGHT of stairs, typing on a keyboard, even holding a pose—requires coordinating the movement of body parts. This is accomplished by the interaction of the nervous system with muscle. The role of the nervous system is to activate the muscles that provide the forces needed to move in a particular way. This is not a simple task. Not only must the nervous system decide which muscles to activate, how much to activate them, and the sequence in which they must be activated in order to move one part of the body, but it must also control the influence of the resultant muscle forces on other body parts and maintain the required posture.

This chapter examines how the nervous system controls muscle force and how the force exerted by a limb depends on muscle structure. We also describe how muscle activation changes to perform different types of movement.

The Motor Unit Is the Elementary Unit of Motor Control

A Motor Unit Consists of a Motor Neuron and Multiple Muscle Fibers

The nervous system controls muscle force with signals sent from motor neurons in the spinal cord or brain stem to the muscle fibers. A motor neuron and the muscle fibers it innervates are known as a motor unit, the basic functional unit by which the nervous system controls movement, a concept proposed by Charles Sherrington in 1925.

A typical muscle is controlled by a few hundred motor neurons whose cell bodies are clustered in a motor nucleus in the spinal cord or brain stem. The axon of each motor neuron exits the spinal cord through the ventral root or through a cranial nerve in the brain stem and runs in a peripheral nerve to the

muscle. When the axon reaches the muscle, it branches and innervates from a few to several thousand muscle fibers (Figure 31–1).

Once synaptic input depolarizes the membrane potential of a motor neuron above threshold, the neuron generates an action potential that is propagated along the axon to its terminals in the muscle. The action potential releases acetylcholine at the neuromuscular synapse, triggering an action potential at the sarcolemma of the muscle fiber (Chapter 12). A muscle fiber has electrical properties similar to those of a large-diameter, unmyelinated axon, and thus, action

potentials propagate along the sarcolemma, although more slowly due to the higher capacitance of the fiber resulting from the transverse tubules (see Figure 31–9). Because the action potentials in all the muscle fibers of a motor unit occur at approximately the same time, they contribute to extracellular currents that sum to generate a field potential near the active muscle fibers.

Most muscle contractions involve the activation of many motor units, whose currents sum to produce signals (*compound action potentials*) that can be detected by electromyography. The electromyogram (EMG) is typically large and can be easily recorded with electrodes
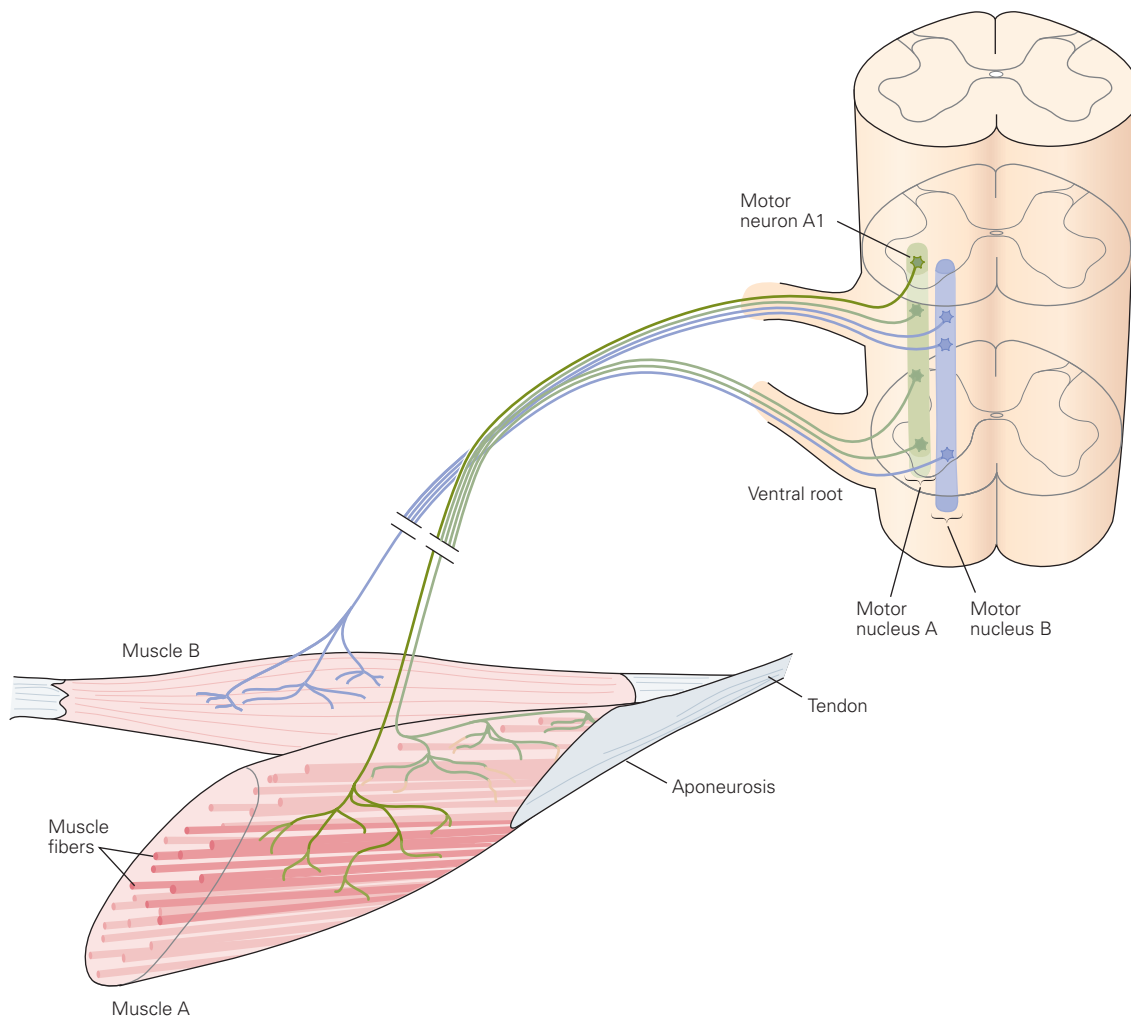
Figure 31–1 A typical muscle consists of many thousands of muscle fibers working in parallel and organized into a smaller number of motor units. A motor unit comprises a motor neuron and the muscle fibers it innervates, illustrated here by motor neuron A1. The motor neurons innervating one muscle are usually clustered into an elongated motor nucleus that may extend over one to four segments within the ventral spinal cord. The axons from a motor nucleus exit the spinal cord in several ventral roots and peripheral nerves but are collected into one nerve bundle near the target muscle. In the figure, motor nucleus A includes all those motor neurons innervating muscle A; likewise, motor nucleus B includes all the motor neurons that innervate muscle B. The extensively branched dendrites of each motor neuron (not shown in the figure) tend to intermingle with those of motor neurons from other nuclei.

placed on the skin over the muscle. The timing and amplitude of EMG activity, therefore, reflect the activation of muscle fibers by the motor neurons. EMG signals are useful for studying the neural control of movement and for diagnosing pathology (Chapter 57).

Each fiber in most mature vertebrate muscles is innervated by a single motor neuron. The number of muscle fibers innervated by one motor neuron, the *innervation number*, varies across muscles. In human skeletal muscles, the innervation number ranges from average values of 5 for an eye muscle to 1,800 for a leg muscle (Table 31–1). Because innervation number denotes the number of muscle fibers within a motor unit, differences in innervation number determine the differences in increments in force produced by activation of different motor units in the same muscle. Thus, the innervation number also indicates the fineness of control of the muscle at low forces; the smaller the innervation number, the finer the control achieved by varying the number of activated motor units.

The differences in innervation numbers between motor units in the same muscle can be substantial. For example, motor units of the first dorsal interosseous muscle of the hand have innervation numbers ranging

Table 31–1 Innervation Numbers in Human Skeletal Muscles

Muscle	Alpha motor axons	Muscle fibers	Average innervation number
Biceps brachii	774	580,000	750
Brachioradialis	333	129,200	410
Cricothyroid	112	18,550	155
Gastrocnemius (medial)	579	1,042,000	1,800
Interossei dorsales (1)	119	40,500	340
Lumbricales (1)	96	10,269	107
Masseter	1,452	929,000	640
Opponens pollicis	133	79,000	595
Platysma	1,096	27,100	25
Posterior cricoarytenoid	140	16,200	116
Rectus lateralis	4,150	22,000	5
Temporalis	1,331	1,247,000	936
Tensor tympani	146	1,100	8
Tibialis anterior	445	272,850	613
Transverse arytenoid	139	34,470	247

Source: Adapted, with permission, from Enoka 2015. © Human Kinetics, Inc.

from approximately 21 to 1,770. The strongest motor unit in the hand's first dorsal interosseous muscle can exert approximately the same force as the average motor unit in the leg's medial gastrocnemius muscle due to different ranges of innervation numbers in the two muscles.

The muscle fibers of a single motor unit are distributed throughout the muscle and intermingle with fibers innervated by other motor neurons. The muscle fibers innervated by a single motor unit can be distributed across 8% to 75% of the volume in a limb muscle, with 2 to 5 muscle fibers belonging to the same motor unit among 100 muscle fibers. Therefore, the muscle fibers in a cross-section through the middle of an entire muscle are associated with 20 to 50 different motor units. This distribution and even the number of motor units change with age and with some neuromuscular disorders (Chapter 57). For example, muscle fibers that lose their innervation after the death of a motor neuron can be reinnervated by collateral sprouts from neighboring axons.

Some muscles comprise discrete compartments that are each innervated by a different primary branch of the muscle nerve. Branches of the median and ulnar nerves in the forearm, for example, innervate distinct compartments in three multitendon extrinsic hand muscles that enable the fingers to be moved relatively independently. The muscle fibers belonging to each motor unit in such muscles tend to be confined to one compartment. A muscle can therefore consist of several functionally distinct regions.

The Properties of Motor Units Vary

The force exerted by a muscle depends not only on the number of motor units that are activated during a contraction but also on three properties of motor units: contraction speed, maximal force, and fatigability. These properties are assessed by examining the force exerted by individual motor units in response to variations in the number and rate of evoked action potentials.

The mechanical response to a single action potential is known as a *twitch contraction.* The time it takes the twitch to reach its peak force, the *contraction time,* is one measure of the contraction speed of the muscle fibers that compose a motor unit. The motor units in a muscle typically exhibit a range of contraction times from slow to fast contracting. The mechanical response to a series of action potentials that produce overlapping twitches is known as a *tetanic contraction* or *tetanus.*

The force exerted during a tetanic contraction depends on the extent to which the twitches overlap

and summate (ie, the force varies with the contraction time of the motor unit and the rate at which the action potentials are evoked). At lower rates of stimulation, the ripples in the tetanus denote the peaks of individual twitches (Figure 31–2A). The peak force achieved during a tetanic contraction varies as a sigmoidal function of action potential rate, with the shape of the curve depending on the contraction time of the motor unit (Figure 31–2B). Maximal force is reached at lower action potential rates for slow-contracting motor units than the rates needed to achieve maximal force in fast-contracting units.

The functional properties of motor units vary across the population and between muscles. At one end of the distribution, motor units have long twitch contraction times and produce small forces, but are less fatigable. At the other end of the distribution, motor units have short contraction times, produce large forces, and are
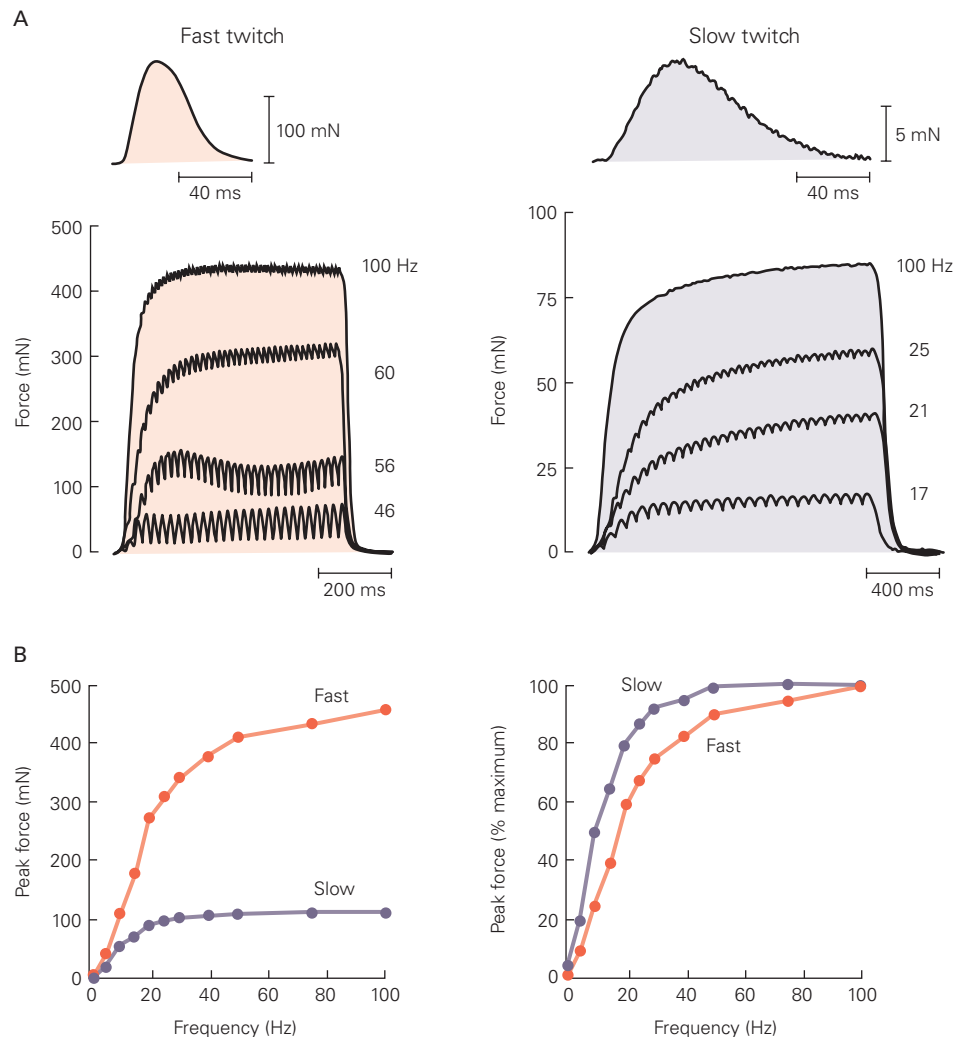
Figure 31–2 The force exerted by a motor unit varies with the rate at which its neuron generates action potentials.

A. Traces show the forces exerted by fast- and slow-contracting motor units in response to a single action potential (**top trace**) and a series of action potentials (set of **four traces below**). The time to the peak twitch force, or contraction time, is briefer in the faster unit. The rates of the action potentials used to evoke the tetanic contractions range from 17 to 100 Hz in the slow-contracting unit to 46 to 100 Hz in the fast-contracting unit. The peak tetanic force evoked by 100-Hz stimulation is greater for the fast-contracting unit. Note the different force scales for the two sets of traces. (Adapted, with permission, from Botterman, Iwamoto, and Gonyea 1986; adapted from Fuglevand, Macefield, and Bigland-Ritchie 1999; and Macefield, Fuglevand, and Bigland-Ritchie 1996.)

B. Relation between peak force and the rate of action potentials for fast- and slow-contracting motor units. The absolute force (*left plot*) is greater for the fast-contracting motor unit at all frequencies. At lower stimulus rates (*right plot*), the force evoked in the slow-contracting motor unit (longer contraction time) sums to a greater relative force (percent of peak force) than in the fast-contracting motor unit (shorter contraction time).