unexpected motions of the boat evoke automatic postural responses that prevent falls. Before you reach out to place a glass on the table, your nervous system makes anticipatory postural adjustments to maintain your balance.

Somatosensory, vestibular, and visual information are integrated to provide a coherent sense of the position and velocity of the body in space with respect to the support surface, gravity, and visual environment. Since the surface is unstable and vision is not providing earth-stable information, your dependence on vestibular information is greater than usual. Your head is kept stable while your trunk motions and walking pattern adjust for disequilibrium caused by the moving surface. You notice that both your voluntary tasks and your balance control deteriorate when trying to attend to both goals.

Equilibrium and Orientation Underlie Posture Control

Postural equilibrium refers to the ability to actively stabilize the upper body by resisting external forces acting on the body. Although the dominant external force affecting equilibrium on earth is gravity, other inertial forces and external perturbations must also be resisted. Depending on the particular task or behavior, different sets of muscles are activated in response to or in anticipation of disturbance to equilibrium.

Postural orientation refers to the ability to actively align body segments, such as the trunk and head, with respect to each other and to the environment. Depending on the particular task or behavior, body segments may be aligned with respect to gravitational vertical, visual vertical, or the support surface. For example, when skiing downhill, the head may be oriented to gravitational and inertial vertical, but not to the visual or support surface references that are inclined.

The biomechanical requirements of postural control depend on anatomy and postural orientation and thus vary among species. Nevertheless, in a variety of species, the control mechanisms for postural equilibrium and orientation have many common features. The sensorimotor mechanisms for postural control are quite similar in humans and quadrupedal mammals even though their habitual stance is different.

Postural Equilibrium Controls the Body's Center of Mass

With many segments linked by joints, the body is mechanically unstable. To maintain balance, the nervous system must control the position and motion of the body's *center of mass* as well as the body's rotation about it. The center of mass is a point that represents the average position of the body's total mass. In the standing adult, for example, the center of mass is located about 2 cm in front of the second lumbar vertebra; in a young child, it is higher. The location of the center of mass is not fixed but depends on postural orientation. For example, when you flex at the hips while standing, the center of mass moves from a location inside the body to a position outside the body.

Although gravity pulls on all body segments, the net effect on body equilibrium acts through the body's center of mass. The force due to gravity is opposed by the forces between the feet and the ground. Each point on the surface will generate a force on the foot. All the forces acting between the foot and the ground can be summed to yield a single force vector termed the *ground reaction force*. This origin of the ground reaction force vector on the surface is the point at which the rotational effect of all the forces on the feet are balanced and is termed the *center of pressure* (Box 36–1).

Maintaining balance while standing requires keeping the downward projection of the center of mass within the base of support, an imaginary area defined by those parts of the body in contact with the environment. For example, the two feet or one foot of a standing human define a *base of support* (Box 36–1). However, when a standing person leans against a wall or is supported by crutches, the base of support extends from the ground under the feet to the contact point between the body and the wall or crutches. Because the body is always in motion, even during stable stance, the body's center of mass continually moves about with respect to the base of support. Postural instability is determined by how fast the center of mass is accelerating toward and beyond the boundary of its base of support and how close the downward projection of the body's center of mass is to the boundary.

Upright stance requires two actions: (1) maintaining support against gravity by keeping the center of mass at some height and joints stable and (2) maintaining balance by controlling the trajectory of the center of mass in the horizontal plane. Balance and antigravity support are controlled separately by the nervous system and may be differentially affected in certain pathological conditions. For example, antigravity support can be excessive when spasticity is present after a stroke or insufficient in the hypotonia of cerebral palsy, although balance control may be preserved. Alternatively, in vestibular disorders, antigravity support can be normal, although balance control is disordered.

Box 36–1 Center of Pressure

The center of pressure (CoP) is defined as the origin of the *ground reaction force* vector on the support surface. For the body to be in static equilibrium, that is, to remain motionless, the force caused by gravity and the ground reaction force must be equal and opposite, and the CoP must be directly under the center of mass (CoM) (Figure 36–1A). Misalignment of the CoM and CoP causes motion of the CoM. For example, if the CoM projection onto the base of support is to the right of the CoP, the body will sway to the right until the CoP moves to the right to move the CoM back over the base of support.

However, standing is never truly static. While the body is in motion (postural sway), CoM and CoP are not aligned and dynamic equilibrium must maintain balance (Figure 36–1B). In fact, when the body is unsupported, CoP and CoM are continually in motion and are rarely aligned, although when averaged over time during quiet stance, they are coincident. The sway of the body during quiet stance can be described by the trajectory of either CoM or CoP over time, such as sway path, area, velocity, and frequency.

In more dynamic situations like walking, running, turning, and jumping, stability can be achieved even when the CoM briefly goes outside the base of support. For example, when standing on one leg or on a narrow beam, momentum from rotating the hips, arms, and other body parts or movement of the CoP can be used to change the direction of the ground reaction force to return the body CoM over its base of support to maintain stability (Figure 36–1B). If the CoM is outside the base of support and heading away from it, subjects may need to take a step or grab a stable object to change the base of support and avoid a fall.

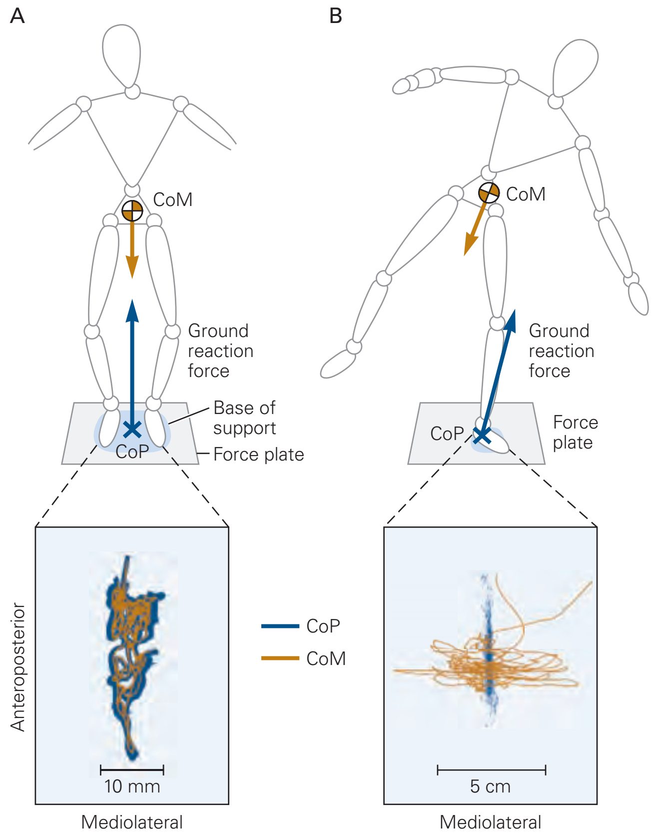

Figure 36–1 The center of mass is controlled by moving the center of pressure.

A. The force caused by gravity passes through the center of mass (**CoM**) in the trunk. The surface exerts an upward force against each foot, such that the ground reaction force vector originates at the center of pressure (**CoP**) on the support surface. **Below:** Even when the feet remain in place, the CoP (**blue displacement**) and CoM (**gold displacement**) are always in motion as we sway. During normal standing on two feet, the projection of the CoM of the body remains within the base of support (**light blue rectangle** around the feet in contact with the ground) for equilibrium. The base of support of the standing human is defined by contact of the feet on the support surface.

B. In a dynamic situation, such as standing on one leg on a narrow beam, equilibrium can be maintained even when the body CoM displacements (**gold displacements**) go outside of the base of support for brief periods. Strategies such as counter-rotation of the lower and upper body can tilt the ground reaction force so that it accelerates the body CoM back over its base of support. (Adapted, with permission, from Otten 1999. Permission conveyed through Copyright Clearance Center, Inc.)

Antigravity support, or "postural tone," is provided by the tonic activation of muscles that generate force against the ground to keep the trunk and limbs extended and the center of mass at the appropriate height. In humans, much of the support against gravity is provided by passive bone-on-bone forces in joints such as the knees, which can be fully extended during stance, and in stretched ligaments such as those at the front of the hips. Nevertheless, antigravity support in humans also requires active tonic muscle contraction, for example, in ankle, trunk, and neck extensors. Postural tone, however, should not be considered a static state of muscle activation, as can be seen in pathologies such as decerebrate rigidity or the rigidity of parkinsonism. Normal postural tone is constantly changing, as a "wave" or "reed in the wind," to accommodate changes in postural alignment, voluntary movements, and task requirements.

Postural tone is not sufficient, however, for maintaining balance. Both bipeds and quadrupeds are inherently unstable, and their bodies sway during quiet stance. Actively contracted muscles exhibit a spring-like stiffness that helps to resist body sway, but muscle stiffness alone is insufficient for maintaining balance. Even stiffening of the limbs through muscle co-contraction is not sufficient for balance control. Instead, complex patterns of muscle activation produce direction-specific forces to control the body's center of mass. Body sway caused by even subtle movements, such as the motion of the chest during breathing, is actively counteracted by alterations in postural tone.

Postural Orientation Anticipates Disturbances to Balance

Postural orientation is the manner in which body parts are aligned with respect to each other and to the environment. Animals arrange their bodies to accomplish specific tasks efficiently. Although this postural orientation interacts with balance control, the two systems can act independently. For example, soccer goalies may orient their body to intercept a ball by sacrificing the goal of maintaining balance. In contrast, a patient with Parkinson disease or thoracic kyphosis may use an inefficient, flexed postural alignment to maintain effective control of balance while standing.

The energy needed to maintain body position over a period of time can influence postural orientation. In humans, for example, the upright orientation of the trunk with respect to gravity minimizes the forces and thus the energy required to hold the body's center of mass over the base of support. Task requirements also affect postural orientation. For some tasks, it is important to stabilize the arrangement of the body in space, whereas for others, it is necessary to stabilize one body part with respect to another. When walking while carrying a full glass, for example, it is important to stabilize the hand against gravity to prevent spillage. In contrast, when walking while reading a cell phone, the hand must be stabilized with respect to the head and eyes to maintain visual acuity.

Subjects may adopt a particular postural orientation to optimize the accuracy of sensory signals regarding body motion. For example, when standing and walking inside a ship, in which the surface and visual references may be unstable, information about earth vertical is derived primarily from vestibular inputs. A person often aligns his head with respect to gravitational vertical when balancing on an unstable surface because the perception of vertical is most accurate when the head is upright and stable.

Anticipatory alterations of habitual body orientation can minimize the effect of a possible disturbance. For example, people often lean in the direction of an anticipated external force, or they flex their knees, widen their stance, and extend their arms when anticipating that stability will be compromised.

Postural Responses and Anticipatory Postural Adjustments Use Stereotyped Strategies and Synergies

When a sudden disturbance causes the body to sway, various postural motor strategies are used to maintain the center of mass within the base of support. In one strategy, the base of support remains fixed relative to the support surface: While the feet remain in place, the body rotates about the ankles back to the upright position (Figure 36–2A). In other strategies, the base of support is moved or enlarged, for example, by taking a step or by grabbing a support with the hand (Figure 36–2B).

Older views of motor control focused on trunk and proximal limb muscles as the main postural effectors. Recent behavioral studies show that any group of muscles from the neck and trunk, legs and arms, or feet and hands can act as postural muscles depending on the body parts in contact with the environment and the biomechanical requirements of equilibrium.

When studying the posture control system, scientists disrupt balance in a controlled manner to determine the subject's automatic postural response. This response is described by the ground reaction force vector, the motion of the center of pressure, and movements of parts of the body. The electrical activity

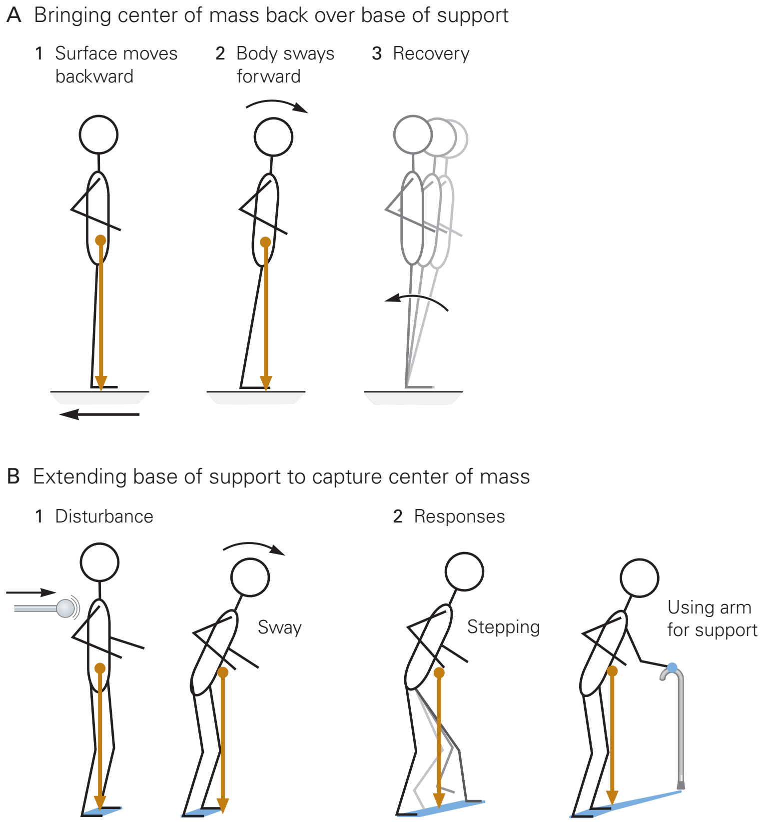

Figure 36–2 Automatic postural responses keep the center of mass within the base of support.

A. One postural strategy for regaining balance is to bring the center of mass back to its origin over the base of support. When the platform on which a subject is standing is suddenly moved backward, the body sways forward and the projection of the center of mass moves toward the toes. During recovery, the body actively exerts force into the surface about the ankles, bringing the center of mass back to the original position over the feet.

B. An alternative postural strategy enlarges the base of support to keep the center of mass within the base. A disturbance causes the subject to sway forward and the center of mass moves toward the boundary of the base of support (**blue area** on the ground). The base can be enlarged in two ways: taking a step and placing the foot in front of the center of mass to decelerate the body's motion, or grabbing a support and thereby extending the base to include the contact point between the hand and support.

of many muscles is recorded by electromyography (EMG), which reflects the firing of alpha motor neurons that innervate skeletal muscle and thus provides a window into the nervous system's output for balance control. The combination of all these measurements allows investigators to infer the active neural processes underlying balance control.

Automatic Postural Responses Compensate for Sudden Disturbances

An automatic postural response to a sudden disturbance is not a simple stretch reflex but rather the synergistic activation of a group of muscles in a characteristic sequence with the goal of maintaining equilibrium. That is, the recruitment of a muscle for a postural response serves the requirements of equilibrium and is not a reflexive change in the muscle's length caused by the disturbance. For example, when the surface under a person is rotated in the toes-up direction, the ankle extensor (gastrocnemius) is lengthened and a small stretch reflex may occur. However, the postural response for balance recruits the antagonist ankle flexor (tibialis anterior), which itself is shortened by the surface rotation, while suppressing the stretch response in the gastrocnemius. In contrast, when the platform is moved backward, the gastrocnemius is again lengthened but now it is recruited for the postural response, as evidenced by a second burst of EMG activity after the stretch reflex. Thus, the initial change in length of a muscle induced by perturbation does not determine whether that muscle is recruited for postural control, and stretch reflexes are not the basis for postural control. In fact, monosynaptic stretch reflexes are too weak to move the body center of mass effectively, and very often, the postural muscles activated to recover equilibrium have not been stretched.

Automatic postural responses to sudden disturbances have characteristic temporal and spatial features. A postural response in muscles must be recruited rapidly following the onset of a disturbance. Sudden movement of the support surface under a standing cat evokes EMG activity within 40 to 60 ms (Figure 36–3). Humans have longer latencies of postural response (90–120 ms in the ankle muscles); the increased delay is attributed to the larger body size of humans and thus

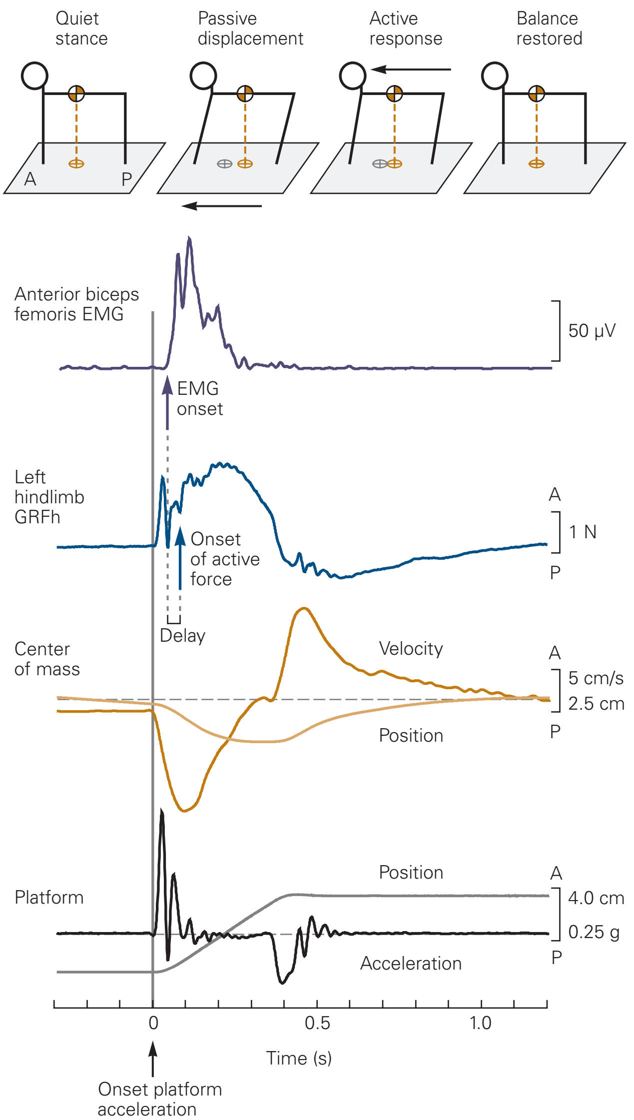

Figure 36–3 Automatic postural responses have stereotypical temporal characteristics. Electromyographic (**EMG**) activity has a characteristic latency. Anterior motion of the platform evokes an EMG response in the hip extensor muscle (anterior biceps femoris) of a cat approximately 40 ms after the onset of platform acceleration (100 ms in a human). This latency is stereotyped and repeatable across subjects and is approximately four times as long as that of the monosynaptic stretch reflex. As the platform moves, the paws are carried forward and the trunk remains behind owing to inertia, causing the center of mass to move backward with increasing velocity with respect to the platform. The velocity of the center of mass peaks and then decreases as the horizontal component of the ground reaction force (**GRFh**) increases following muscle activation. The delay of approximately 30 ms between the onset of EMG activity and the onset of the active response reflects excitation–contraction coupling and musculoskeletal compliance. The automatic postural response extends the hind limb, propelling the trunk forward and restoring the position of the center of mass with respect to the paws. (Abbreviations: **A**, anterior; **P**, posterior.) (Data from J. Macpherson.)

the greater signal conduction distances from sensory receptors to the central nervous system and thence to leg muscles. The latency of automatic postural responses is shorter than voluntary reaction time but longer than the monosynaptic stretch reflex.

Postural responses involving a change in support base, such as stepping, have even longer latencies than those that occur when the feet remain in place. The longer time presumably affords greater flexibility in the commands transmitted by long loops through the cortex; for example, the choice of foot to begin the step, the direction of the step, and the path of the step around obstacles.

Activation of postural muscles results in contraction and the development of force in the muscles, leading to torque (rotational force) at the joints. The net result is an active response, the ground reaction force (Box 36–1), that restores the center of mass to its original position over the base of support (Figure 36–3). The delay between EMG activation and the active response, approximately 30 ms in the cat and 50 ms in humans, reflects the excitation–contraction coupling time of each muscle as well as the compliance of the musculoskeletal system.

The amplitude of EMG activity in a particular muscle depends on both the speed and direction of postural disturbance. The amplitude increases as the speed of a movable platform under a standing human or cat increases, and it varies in a monotonic fashion as the direction of platform motion is varied systematically. Each muscle responds to a limited set of perturbation directions with a characteristic tuning curve (Figure 36–4).

Although individual muscles have unique directional tuning curves, muscles are not activated independently but instead are activated together in *synergies*, with characteristic time delays. The muscles within a synergy receive a common command signal during postural responses. In this way, the many muscles of the body are controlled by just a few signals, reducing the time needed to compute the appropriate postural response (Box 36–2).

The set of muscles recruited in a postural response to a disturbance depends on the body's initial stance. The same disturbance elicits very different postural responses in someone standing unaided, standing while grasping a stable support, or crouching on all four limbs. For example, forward sway activates muscles in the back of the legs and trunk during upright free stance. When the subject is holding onto a stable support, muscles of the arms rather than those of the legs are activated first. When the subject is crouched on toes and fingers, like a cat, muscles in the front of the legs and in the arms are activated (Figure 36–6A).

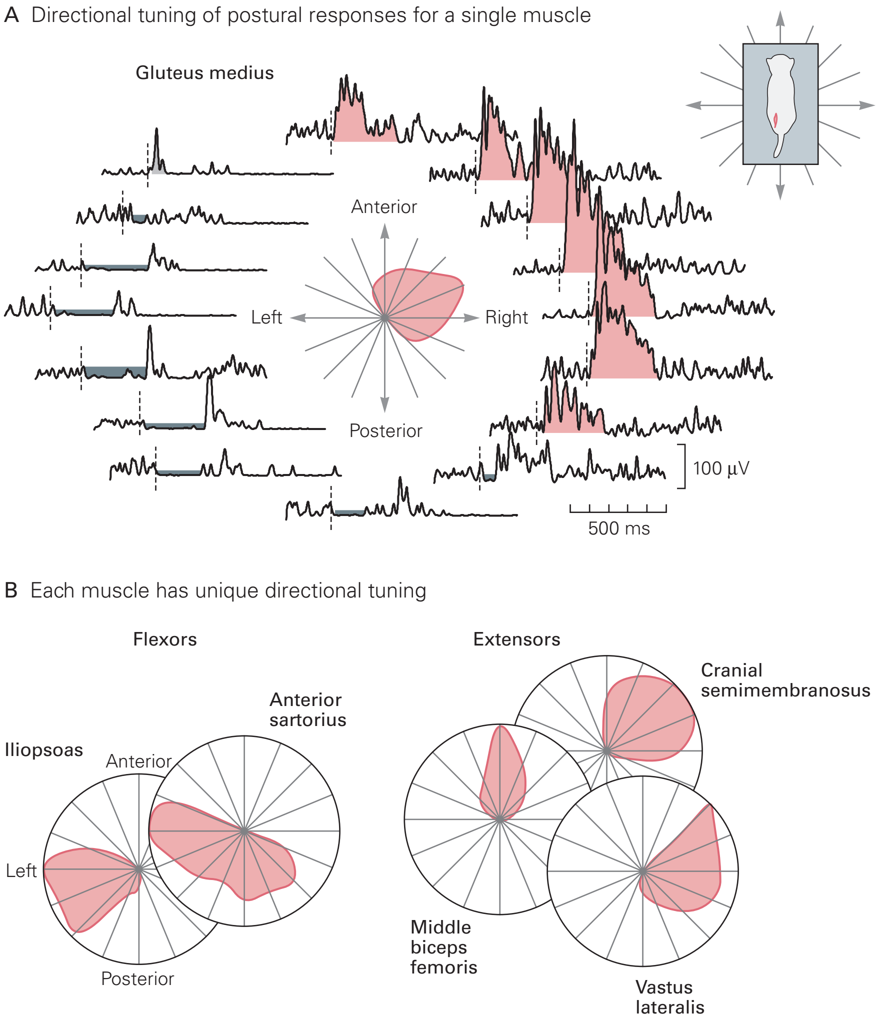

Figure 36–4 **Automatic postural responses have stereotypical directional characteristics.** (Adapted from Macpherson 1988.)

A. The gluteus medius muscle in the cat, a hip extensor and abductor, responds to a range of directions of motion in the horizontal plane. The electromyographic (EMG) records shown here are from a cat standing on a platform that was moved in the horizontal plane in each of 16 evenly spaced directions. The gluteus medius muscle of the left hind limb was activated by motion in several directions (**pink**) and inhibited in the remaining directions (**gray**). The **dashed vertical lines** indicate the onset of platform acceleration. In the center is a polar plot of the amplitude of EMG activity versus the direction of motion during the automatic postural response; it represents a directional tuning curve for the muscle. EMG amplitude was computed from the area under the curve during the first 80 ms of the response.

B. Every muscle has a characteristic directional tuning curve that differs from that of other muscles, even if they have similar actions. The middle biceps femoris and cranial semimembranosus, for example, are both extensors of the hip.

Because postural responses are influenced by recent experience, they adapt only gradually to new biomechanical conditions. When forward sway is induced by backward motion of a platform on which a subject is standing, the posterior muscles of the ankle, knee, and hip are activated in sequence beginning 90 ms after the platform starts moving. This postural response, the *ankle strategy*, restores balance primarily by rotating the body about the ankle joints. However, when forward sway is induced by backward motion of a narrow beam, it is impossible to use surface torque alone to recover equilibrium and the anterior muscles of the hip and trunk are activated. This postural response, the *hip strategy*, restores the body's center of mass by bending forward at the hip joints and counter-rotating at the ankles (Figure 36–6B).

When a subject moves from standing on a wide platform to a narrow beam, she or he persists in using the ankle strategy in the first few trials. This strategy does not work when standing on the beam, and the subject falls. Over several trials, the subject will gradually switch to using the hip strategy. Similarly, moving from the beam back to the platform requires several trials to adapt the postural response back to the ankle strategy (Figure 36–6C).

Although sensory stimulation changes immediately after subjects move from the beam to the floor, the postural response adjusts gradually as it is tuned for optimal behavior by trial and error. If postural responses were simple reflexes, they would change immediately upon a change in sensory drive. Trial-to-trial changes in postural behavior generally occur at the subconscious level (implicit learning) and involve updating of the body schema and internal model of the world within the right parietal cortex. This body schema is dynamic, as it is constantly updated based on experience.

Postural responses not only improve with practice, but the improvements are retained, a sign of motor

Box 36–2 Synergistic Activation of Muscles

Coordinated movements require precise control of the many joints and muscles in the body. Maintaining control is biomechanically complex, in part because different combinations of joint rotations and muscle activations can achieve the same goal. Such redundancy confers great flexibility, for example, in modifying stepping patterns to negotiate obstacles in our path, but comes at the cost of increased complexity in the brain's computation of movement trajectories and forces.

Many factors must be included in the computation of movement commands, including the effect of external forces such as gravity and the forces that one body segment exerts on another during motion. All these factors come into play when the brain computes postural responses to sudden disturbances, but with the added constraint of a time limit on computation: Responses must occur within a certain time or balance will be lost.

It has long been believed that the brain simplifies the control of movement by grouping control variables, for example, activating several muscles together. Using mathematical techniques that parse complex data into a small number of components, one can determine that only four synergies are needed to account for the vast majority of activation patterns of 13 muscles of the human leg and trunk during automatic postural responses to many directions of platform motion (Figure 36–5). Activation of each synergy produces a unique direction of force against the ground, suggesting that postural control is based on task-related variables such as the force between foot and ground rather than the contraction force of individual muscles.

Like the arrangement of notes in a musical chord, each muscle synergy specifies the timing and amplitude of activation for a particular muscle together with others. Just as one note belongs to several different chords, each muscle belongs to more than one synergy. When several chords are played simultaneously, the chord structure is no longer evident in the multitude of notes. Similarly, when several synergies are activated concurrently, the observed muscle pattern gives the appearance of unstructured complexity, but a particular muscle's activation is the result of the systematic addition of synergy commands. Concurrent activation of synergies simplifies the neural command signals for movement as only a few central commands are required instead of a separate command for each muscle, while allowing flexibility and adaptability to postural control.

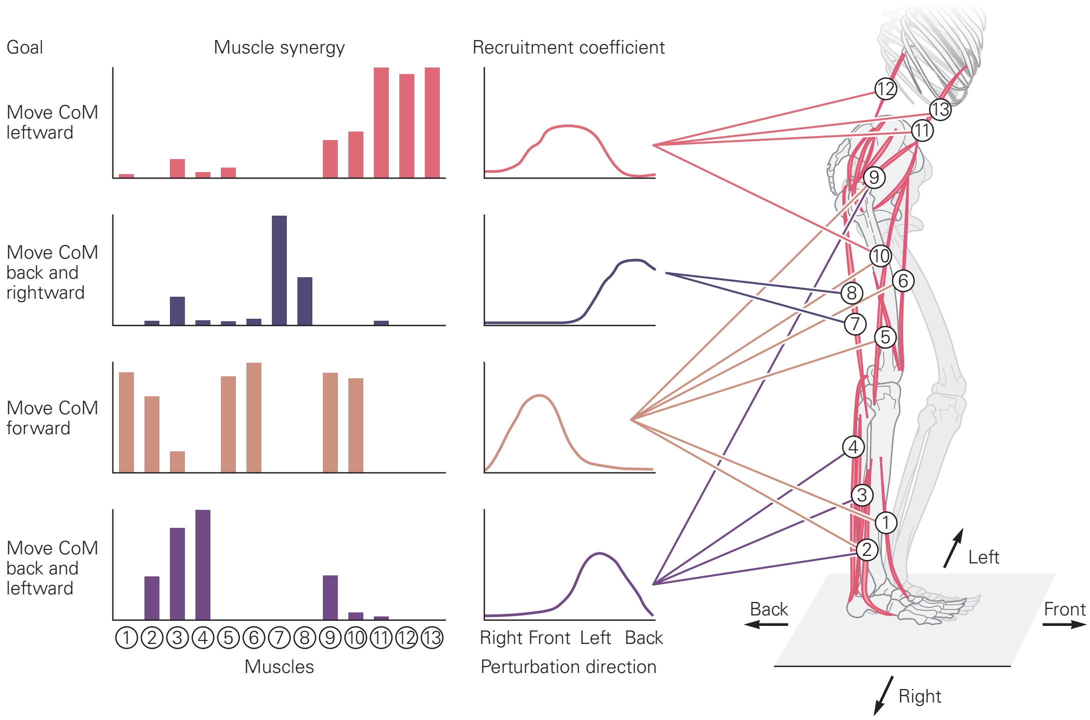

Figure 36–5 Postural commands activate synergies rather than individual muscles. Synergistic activation of several muscles allows movement goals to be translated into specific muscle activity patterns. Each muscle synergy activates a group of muscles in a fixed proportion (**colored bars**) to produce the mechanical output needed to achieve a postural goal. The height of each bar represents the relative amount of activation, or weighting, for each muscle (1–13). Each synergy is activated more or less at particular times during a behavior driven by central commands and sensory drive (recruitment function). For example, different postural synergies are activated for different directions of falling. (Abbreviation: **CoM**, center of mass.) (Reproduced, with permission, from L. Ting.)

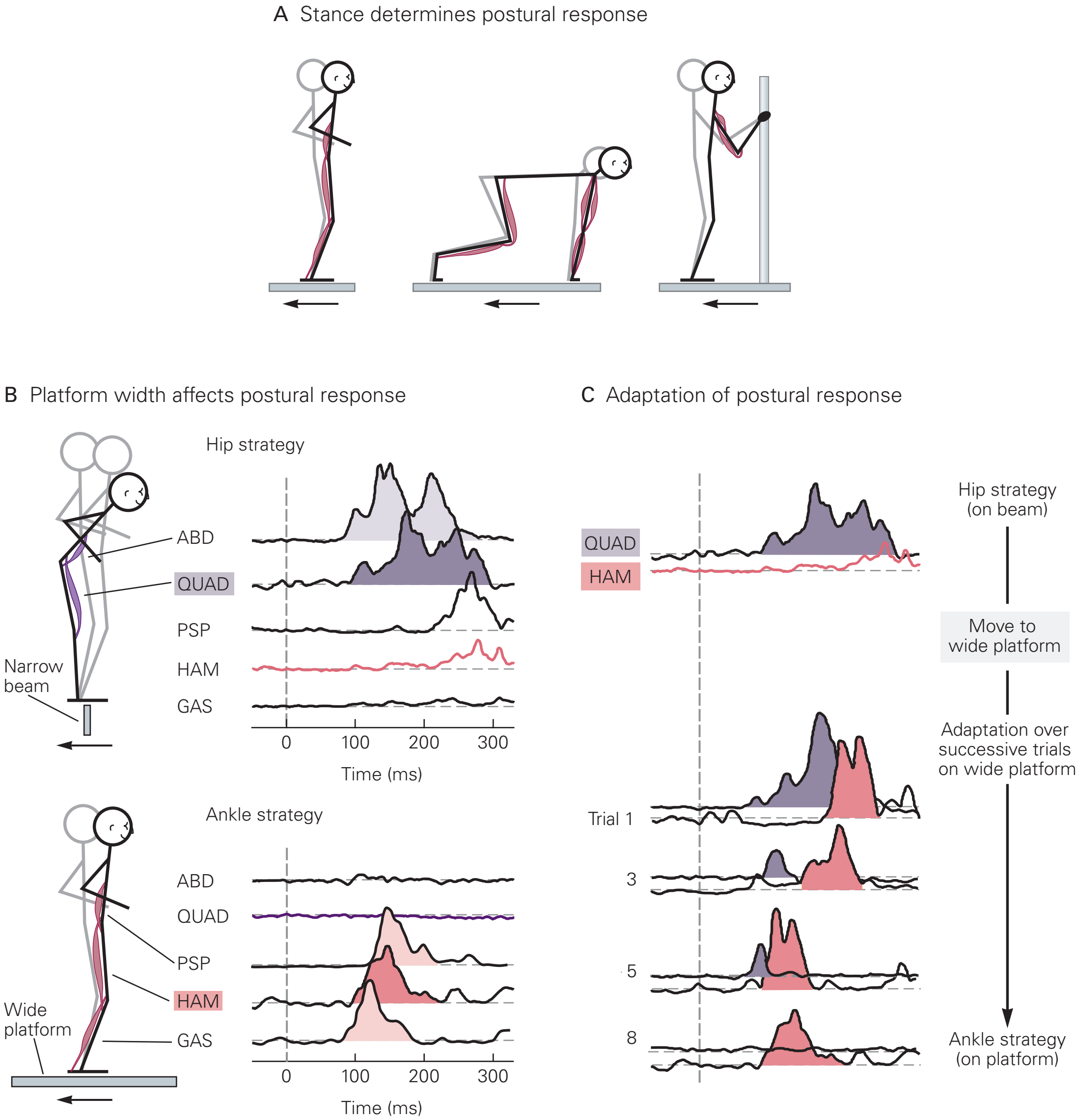

Figure 36–6 Automatic postural responses change with biomechanical conditions.

A. The backward movement of a platform activates different groups of muscles depending on initial stance. **Gray stick figures** show initial positions (upright unsupported, quadrupedal, or upright supported). The muscles activated in each postural response are shown in **red**. (Adapted, with permission, from Dunbar et al. 1986.)

B. When a subject stands on a narrow beam that is abruptly moved backward, the anterior muscles—abdominals (**ABD**) and quadriceps (**QUAD**)—are recruited to flex the trunk and extend the ankles, moving the hips backward (the hip strategy). When the subject instead stands on a wide platform that is moved backward, his posterior muscles—paraspinals (**PSP**), hamstrings (**HAM**), and gastrocnemius (**GAS**)—are activated to bring the body back to the erect position by rotating at the ankles (the ankle strategy). Muscles representative of different postural responses are highlighted in color. **Dashed vertical lines** in the plots indicate onset of platform (or beam) acceleration.

C. Postural strategy adapts after the subject moves from the narrow beam onto the wide platform. On the beam, the quadriceps are activated and the hamstrings are silent; after adaptation to the wide platform, the reverse is observed. The transition from quadriceps to hamstrings activation occurs over a series of trials; the activity in the quadriceps gradually decreases in amplitude, whereas the hamstrings are activated earlier and earlier until, by trial 8, quadriceps activity disappears altogether. Ankle and trunk muscles show similar patterns of adaptation. (B. and C, adapted, with permission, from Horak and Nashner 1986.)

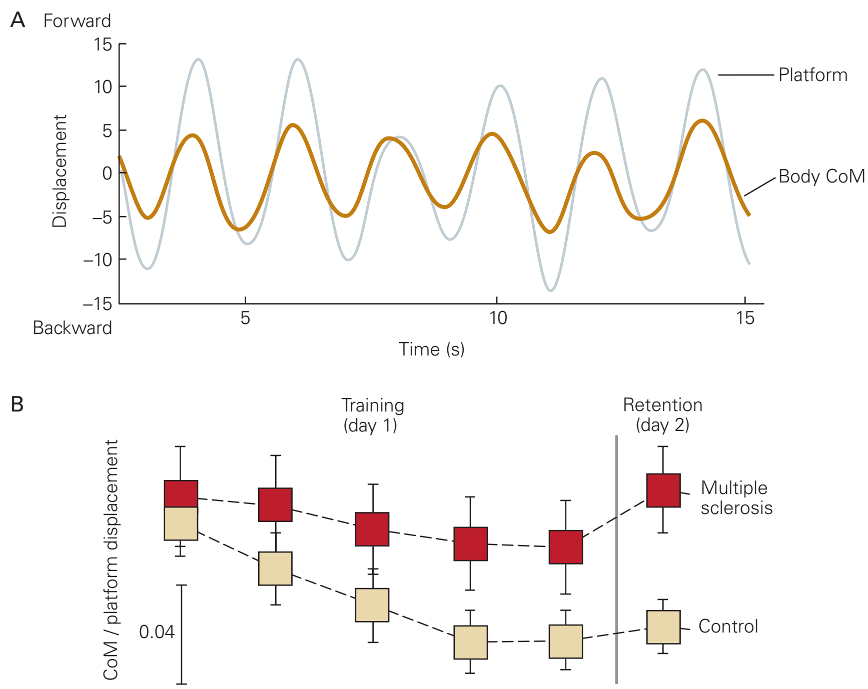

Figure 36–7 Postural responses can be learned and retained with practice.

A. Displacement of body center mass (**CoM, gold oscillation**) in response to forward and backward platform oscillations of varying amplitudes (**gray**) as a healthy subject learns to reduce postural instability.

B. Displacement of the body CoM by forward–backward surface oscillations is reduced across training sessions on day 1, and this improvement is retained on day 2 in healthy control subjects. People with multiple sclerosis also learn to reduce CoM displacements but do not retain this improvement the next day. The mean and standard error of group changes in gain (CoM/surface displacement) are compared. (Adapted, with permission, from Gera et al. 2016.)

learning. For example, when subjects practice standing on an oscillating surface, they gradually learn to decrease the extent of the displacement of their center of mass, and much of this improvement is retained the next day (Figure 36–7). Patients with neurological disorders, such as multiple sclerosis or Parkinson disease, who have significantly impaired postural responses can often learn to improve their postural control with practice, although they may need more practice than normal to retain the improvements (Figure 36–7).

Anticipatory Postural Adjustments Compensate for Voluntary Movement

Voluntary movements can also destabilize postural orientation and equilibrium. For example, rapidly lifting the arms forward while standing produces forces that extend the hips, flex the knees, and dorsiflex the ankles, moving the body's center of mass forward relative to the feet. The nervous system has advance knowledge of the effects of voluntary movement on postural alignment and stability and activates anticipatory postural adjustments, often in advance of the primary movement (Figure 36–8A).

Anticipatory postural adjustments are specific to biomechanical conditions. When a freely standing subject rapidly pulls on a handle fixed to the wall, the leg muscles (gastrocnemius and hamstrings) are activated before the arm muscles (Figure 36–8B). When the subject performs the same pull while his shoulders are propped against a rigid bar, no anticipatory leg muscle activity occurs because the nervous system relies on the support of the bar to prevent the body from moving forward. When the handle is pulled in response to an external cue, the arm muscles are activated faster in the supported condition than in the freestanding condition. Thus, voluntary arm muscle activation is normally delayed when the task requires active postural stability.

Another common preparatory postural adjustment occurs when one begins to walk. The center of mass is accelerated forward and laterally by the unweighting of one leg. This postural adjustment appears to be independent of the stepping program that underlies ongoing locomotion (Chapter 33). Similarly, a forward shift of the center of mass precedes the act of standing on the toes. A subject is unable to remain standing on his toes if he simply activates the calf muscles without moving his center of mass forward; he rises onto his toes only momentarily before gravity restores a flat-footed stance. Moving the center of mass forward over the toes before activating the calf muscles aligns it over the anticipated base of support and thus stabilizes the toe stance.

Postural equilibrium during voluntary movement requires control not only of the position and motion of the body's center of mass but also of the angular momentum about the center of mass. A diver can