41

Posture

The control of posture is crucial for most tasks of daily living. The two components of posture, orientation and balance, require continual adjustment and involve several sensory systems.

To appreciate the complexity of maintaining balance and orientation, imagine that you are waiting tables on a tour boat. You have a tray full of drinks to be delivered to a table on the other side of the rolling deck. Even as your mind is occupied with remembering customer orders, unconscious processes allow you to move about in a smooth and coordinated manner.

The apparently simple task of delivering drinks is supported by a truly complex sensorimotor process for controlling postural orientation and balance. As you cross the deck your brain rapidly processes sensory information and adjusts motor output to maintain your balance, the upright orientation of your head and trunk, and stable arms supporting the tray of full glasses. Before you reach out to place a glass on the table, your nervous system makes anticipatory postural adjustments to maintain your balance. Sudden unexpected motions of the boat evoke automatic postural responses that prevent falls. Somatosensory, vestibular, and visual information is integrated to provide a coherent picture of the position and velocity of the

body in space and to generate and update motor commands that maintain balance and orientation.

Postural Equilibrium and Orientation Are Distinct Sensorimotor Processes

Postural equilibrium, or balance, involves active resistance to external forces acting on the body. The dominant external force affecting equilibrium on earth is gravity. Postural orientation is the positioning of body segments 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.

The biomechanical requirements of postural control depend on anatomy and postural orientation and thus vary with the animal. 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 Requires Control of 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 its center of mass. The center of mass is a point that represents the average position of the body's total mass. In the standing cat, for example, the center of mass is located in the trunk just rostral to the midpoint between forelimbs and hind limbs.

Although gravity pulls on all body segments, the net effect on the body acts through the center of mass. The force of gravity is opposed by the *ground reaction force*, which pushes upward against each foot. The net ground reaction force occurs at an imaginary point on the ground called the *center of pressure* (Box 41–1).

The location of the center of mass in the body is not fixed but depends on postural orientation. When you are standing upright, for example, your center of mass is located in the abdomen approximately 20 mm in front of the second lumbar vertebra. When you flex at the hips, however, the center of mass moves forward to a position outside the body.

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 four paws of a standing cat define a rectangular base of support (see Figure 41–1). When a standing person leans against a wall, the base of support extends from the ground under the feet to the contact point between the body and the wall. Because the body is always in motion, even during stable stance, the 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 moving toward the boundary of its base of support and how close the downward projection of the body's center of mass is to the boundary.

Balance During Stance Requires Muscle Activation

Upright stance requires two actions: (1) maintaining support against gravity (keeping the center of mass at some height) and (2) maintaining balance (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.

Antigravity support, or postural tone, represents the tonic activation of muscles that generate force against the ground to keep the limbs extended and the center of mass at the appropriate height. A cat stands with its limbs in a semiflexed posture (see Figure 41–1) and its extensor muscles are tonically activated to prevent the joints from collapsing into flexion. In humans much of the support against gravity is provided by passive bone-on-bone forces in joints such as the knees, which are 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 muscle contraction, for example in ankle, trunk, and neck extensors. Tonic activation of antigravity muscles is not sufficient, however, for maintaining balance.

Both bipeds and quadrupeds are inherently unstable, and their bodies sway during quiet stance. Actively contracting muscles exhibit a spring-like stiffness that helps to resist body sway, but muscle stiffness alone is insufficient for maintaining balance. Likewise, 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 the posture control system.

Automatic Postural Responses Counteract Unexpected Disturbances

When a sudden disturbance causes the body to sway, various motor strategies are used to maintain the center

Box 41–1 Center of Pressure

The center of pressure is defined as the origin of the ground reaction force vector on the support surface. For the body to be in static equilibrium, the force caused by gravity and the ground reaction force must be equal and opposite, and the center of pressure must be directly under the center of mass.

Misalignment of the center of pressure and center of mass causes motion of the center of mass. If the center of pressure is behind and to the left of the center of mass projection onto the base of support, for example, the body will sway forward and to the right (Figure 41–1).

When no external forces other than gravity are present, the center of pressure and ground reaction force reflect the net effect of muscles activated by the postural system to actively control the center of mass position and therefore balance.

Standing is never truly static. The center of pressure and center of mass are continually in motion and are rarely aligned, although when averaged over time during quiet stance they are coincident. The actual sway of the body during quiet stance is described by the trajectory of the center of mass, not the center of pressure.

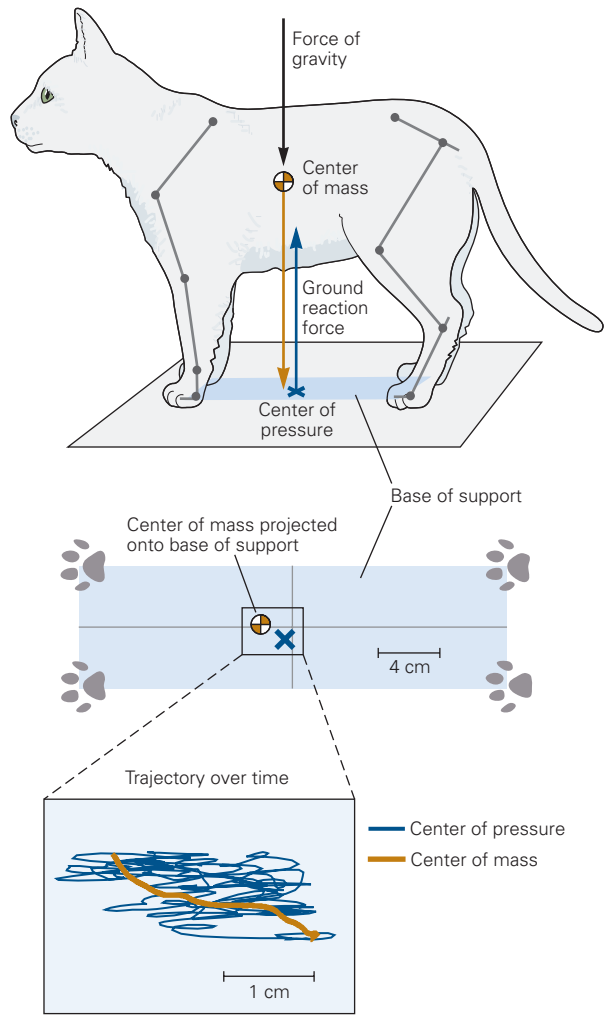


Figure 41–1 The center of mass moves during stance but remains within the base of support. The base of support of the standing cat is defined by the points of contact of the paws on the support surface. The force caused by gravity passes through the center of mass in the trunk. The surface exerts an upward force against each paw, such that the ground reaction force vector originates in the center of pressure on the support surface. Although the paws remain in place, the centers of pressure and mass are always in motion as the cat sways.

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 41–2A). 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 41–2B).

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 under each foot, the motion of the center of pressure, and the movements of the body segments. The electrical activity of many muscles is recorded by electromyography (EMG), which reflects the firing of alpha

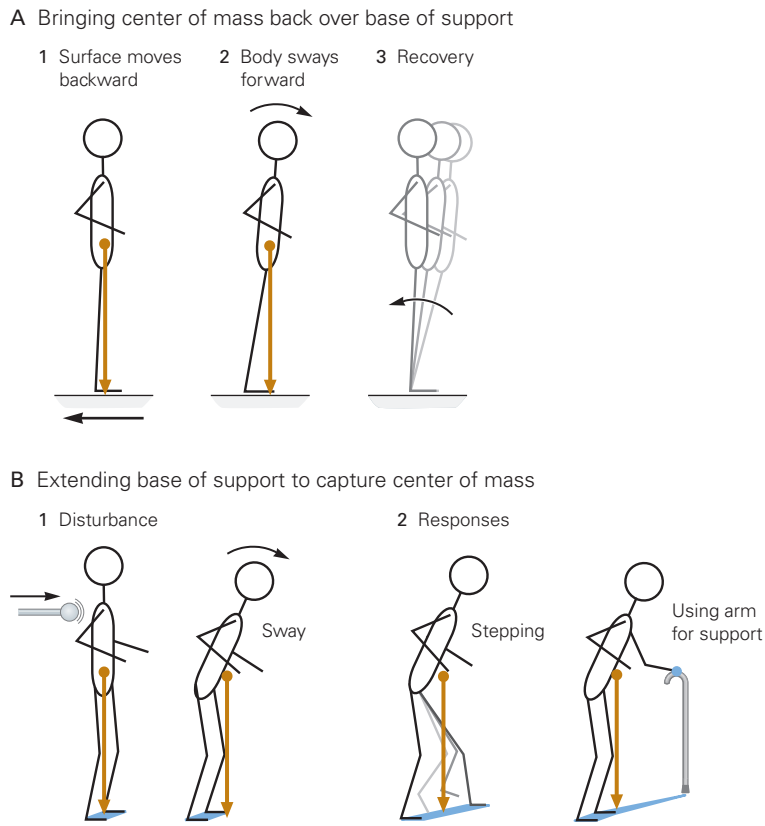


Figure 41–2 Automatic postural responses keep the downward projection of the center of mass within the boundaries of the base of support.

A. One strategy for regaining balance is to bring the center of mass back to its origin on 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 rotates about the ankles, bringing the center of mass back to the original position with respect to the feet.

B. An alternative 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. 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.

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.

An automatic postural response to a sudden disturbance is not a simple reflex but rather the synergistic activation of a group of muscles in a characteristic sequence with the goal of maintaining equilibrium. The recruitment of a muscle during a postural response reflects the requirements of equilibrium rather than the 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. 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.

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 40–60 ms (Figure 41–3). Humans have longer latencies of postural response (80–120 ms); the increased delay is attributed to the larger body size of humans and thus 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 stretch reflex.

Postural responses involving a change in support base, such as stepping, have longer latencies than those that occur when the feet remain in place.

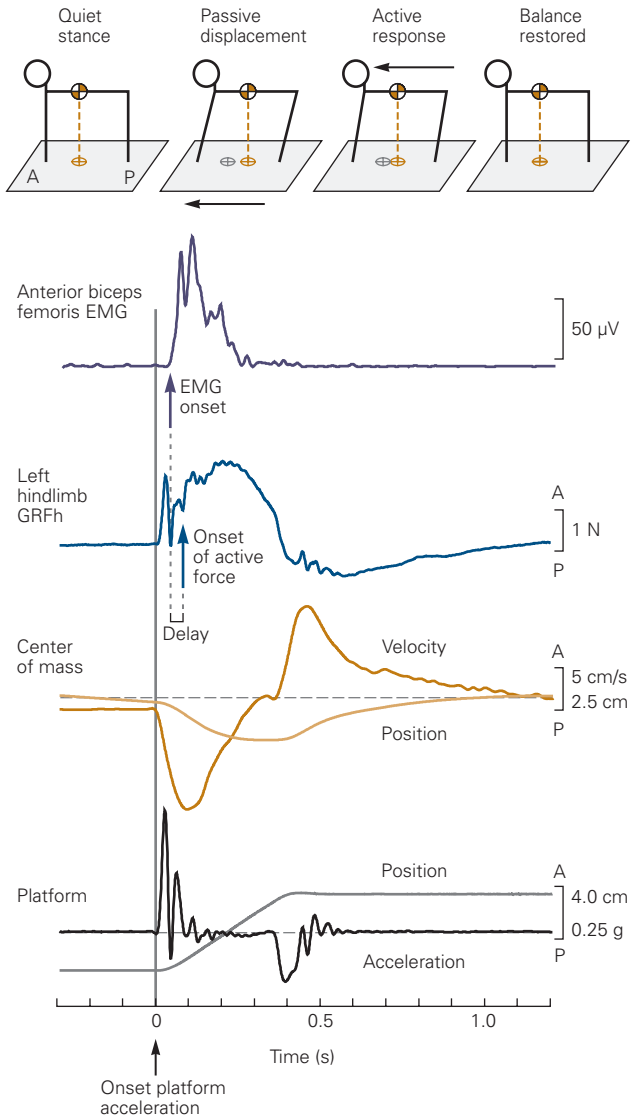


Figure 41–3 Automatic postural responses have stereotypical temporal characteristics. Electromyographic (EMG) activity has a characteristic latency. Anterior motion of the platform evokes an EMG response in the hip extensor muscle (anterior biceps femoris) approximately 40 ms after the onset of platform acceleration. 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 of the cat 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 body 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.

The longer time presumably affords greater flexibility in the response, 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, that restores the center of mass to its original position over the base of support (Figure 41–3). The delay between EMG activation and the active response, approximately 30 ms in the cat, 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 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 41–4).

Although individual muscles have unique directional tuning curves, muscles are not activated independently but instead are coactivated in synergies. 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 41–2).

Automatic Postural Responses Adapt to Changes in the Requirements for Support

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 at 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. When the subject is crouched on toes and fingers, muscles at the front of the legs and in the arms are activated (Figure 41–6A).

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

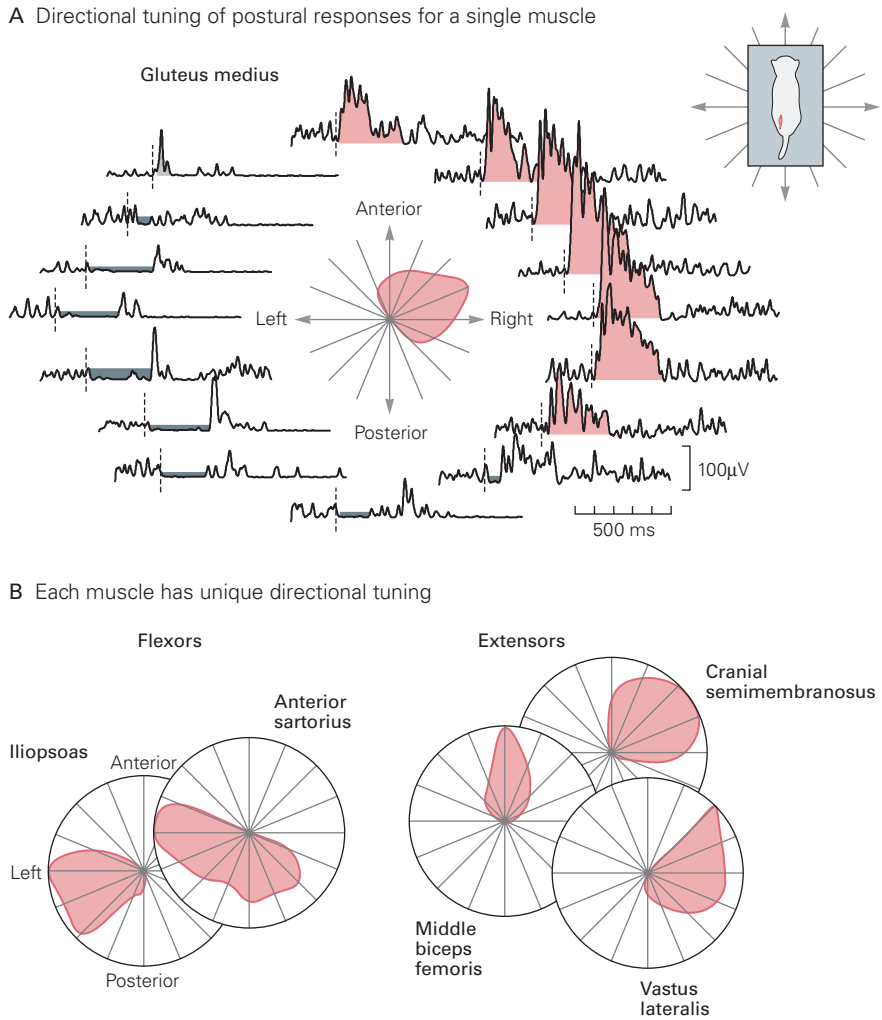


Figure 41–4 Automatic postural responses have stereotypical directional characteristics. (Adapted, with permission, from Macpherson 1988.)

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 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 during the automatic postural response versus the direction of motion; 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.

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, the anterior muscles of the hip and trunk are activated. This postural pattern, the *hip strategy*, restores the body's center of mass by bending forward at the hip joints and counter-rotating at the ankles (Figure 41–6B).

When a subject moves from the wide platform to the narrow beam, 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. He then gradually, over several trials, switches to the hip strategy. Similarly, moving from the beam back to the platform requires several trials to adapt the postural response (Figure 41–6C).

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. Trial-to-trial changes in postural behavior generally occur at the subconscious level and involve updating of the body schema.

Anticipatory Postural Adjustments Compensate for Voluntary Movements

Voluntary movements themselves can destabilize postural orientation and equilibrium. Rapidly lifting the arms forward while standing, for example, 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 41–7A).

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 41–7B). 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. 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.

Locomotion, too, has an important postural component. During walking and running the body is in a constant state of falling as the center of mass moves forward and laterally toward the leg that is in the swing phase. The center of mass is within the base of support during walking only when both feet are on the ground, the double stance phase, and not at all during running. When one foot is supporting the body, the center of mass moves forward in front of the foot, always medial to the base of support. Falling is prevented during walking and running by moving the base of support forward and laterally under the falling center of mass. Postural equilibrium during gait relies on the appropriate placement of each step to control the speed and trajectory of the center of mass (Figure 41–7C). The nervous system plans foot placement several steps in advance using visual information about the terrain and surrounding environment (see Chapter 36).

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 perform elaborate rolls and twists of the body about the center of mass while airborne although the trajectory of his center of mass is fixed once he leaves the board. During swimming and flying the water or air currents in addition to the body's own movements may cause the body to pitch or roll about the center of mass. During voluntary movements postural adjustments control the body's angular momentum by anticipating rotational forces.

Postural Orientation Is Important for Optimizing Execution of Tasks, Interpreting Sensations, and Anticipating Disturbances to Balance

Animals arrange their body parts to accomplish specific tasks efficiently. Although this postural orientation interacts with balance control, the two systems can act independently.

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. Standing cats adopt a characteristic distance between front and back paws that minimizes the energy needed for remaining upright.

Task requirements also affect postural orientation. For some tasks it is important to stabilize the position of a body part 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. When walking while reading a book, the hand must be stabilized with respect to the head and eyes.

Subjects may adopt a particular postural orientation to optimize the accuracy of sensory signals regarding body motion, especially while on unstable or moving surfaces. In activities such as skiing and windsurfing, in which the substrate is unstable, information about earth vertical is derived primarily from vestibular and visual inputs. A person often aligns his head with respect to gravitational vertical because the perception of vertical is most accurate in this position and decreases in accuracy as the head is tilted. The vestibular and visual information regarding the external world, representing an extrinsic coordinate system,

Box 41–2 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 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. In older concepts of synergy the same muscles are always recruited together. This kind of synergy cannot apply to balance responses because each muscle has a unique directional tuning curve and the tuning curves overlap imperfectly (see Figure 41–4B).

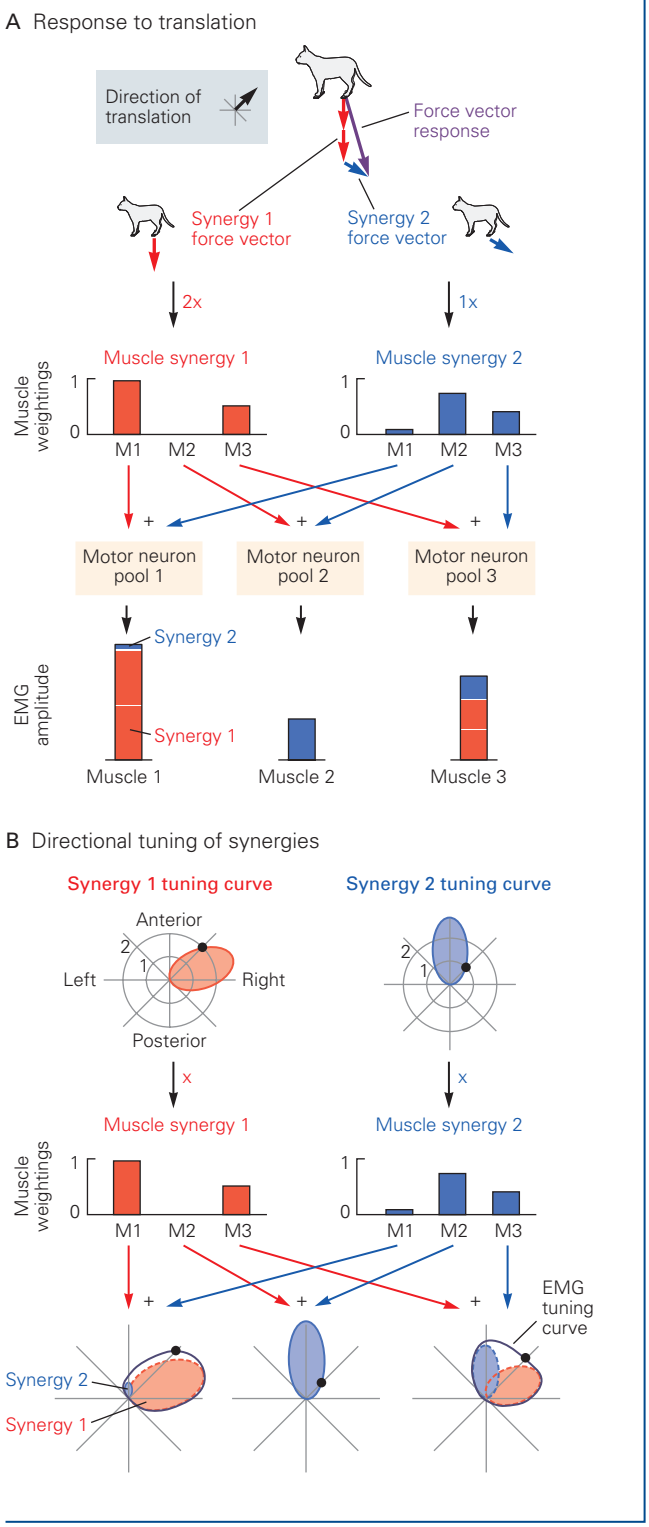
Using mathematical techniques that parse complex data into a small number of components, Lena Ting and Jane Macpherson showed that only four or five synergies are needed to account for the activation patterns of 15 hind limb muscles of the cat during automatic postural responses to many directions of platform motion (Figure 41–5). 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 how a particular muscle should be activated 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. Concurrent activation of synergies nevertheless simplifies the neural command signals for movement while allowing flexibility and adaptability.

Figure 41–5 Postural commands activate synergies rather than individual muscles.

A. The flow chart illustrates two hypothetical synergies that are recruited during the postural response to one direction of translation in the horizontal plane. A posture controller computes the appropriate force vector response for restoring center of mass position and then specifies how much to activate each synergy. Each muscle synergy activates the muscles in a fixed proportion. The height of each bar represents the relative amount of activation, or weighting, for each muscle M1 to M3. Synergy 1 produces a downward force vector by activating M1 strongly, M2 not at all, and M3 moderately. Synergy 2 produces a downward and posterior force vector using the same muscles but with different levels of activation: M1 slightly, M2 strongly, and M3 moderately. When synergy 1 is activated with an amplitude of 2 and synergy 2 an amplitude of 1, the desired force vector response is achieved. Signals from the two muscle synergies are summated in the population of motor neurons innervating each muscle. The contribution of each synergy to the total electromyogram (EMG) activation can be determined.

B. The two hypothetical synergies in part A can generate the unique tuning curves for muscles M1 to M3 in response to all 16 directions of translation in the horizontal plane. The posture controller generates a command signal to each synergy that is tuned to direction of translation (synergy tuning curves). Muscle synergy weightings are multiplied by the synergy amplitudes. Signals from the two synergies are summated at the motor neurons, resulting in EMG activity that is tuned to a direction (the EMG tuning curve). The tuning curve for each of the three muscles is different even though only two synergy commands are used. The contribution of each synergy to the EMG tuning curve of a muscle can also be determined. The **black dots** indicate the amplitudes of the two synergies and resulting EMG activity of the three muscles for the direction illustrated in part A.



is integrated with proprioceptive information, representing an intrinsic coordinate system, to determine the position of the body in space (see Chapter 38). The accuracy of the transformation from intrinsic to extrinsic coordinates may be enhanced if at least one sensory input is aligned with the extrinsic system.

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 surface stability will be compromised.

Sensory Information from Several Modalities Must Be Integrated to Maintain Equilibrium and Orientation

Information about motion from any one sensory system may be ambiguous. Thus multiple sources of sensory information must be integrated in postural centers to determine what orientation and motion of the body in space are appropriate. The influence of any one modality on the postural control system varies according to the task and biomechanical conditions.

According to the prevailing theory, sensory modalities are integrated to form an internal representation of the body that the nervous system uses to plan and execute motor behaviors. Over time this internal representation must adapt to changes associated with early development, aging, and injury.

Somatosensory Afferents Are Important for Timing and Direction of Automatic Postural Responses

Large-diameter, fast somatosensory fibers are critical for maintaining balance during stance. When these axons die, as occurs in some forms of peripheral neuropathy, postural responses to movement of the support surface are delayed, retarding the ground reaction force. As a result, the center of mass moves faster and farther from the initial position and takes longer to return (Figure 41–8). Because it is more likely that the center of mass will move outside the base of support, balance is precarious and a fall may occur. Individuals with large-fiber peripheral neuropathy in the legs accordingly experience ataxia and difficulties with balance.

The somatosensory fibers that give rise to the automatic postural response have not been identified. The largest fibers, those in group I (12–20 μm in diameter), appear to be essential for normal response latencies.

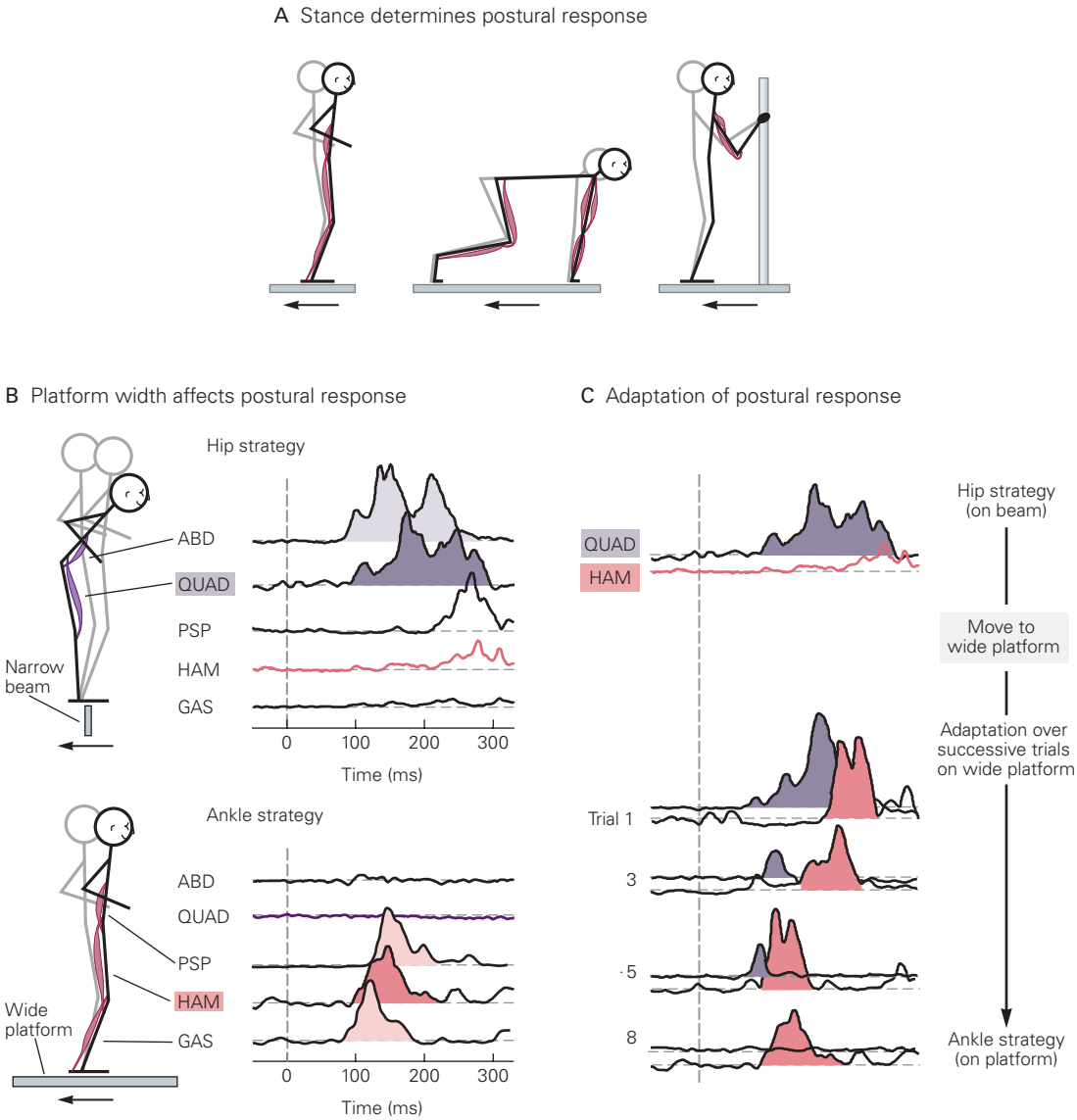


Figure 41–6 Automatic postural responses change with biomechanical conditions.

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 line** indicates 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 occurs over a series of trials; the quadriceps activity gradually decreases in amplitude, whereas the hamstrings are activated earlier and earlier, until by trial eight quadriceps activity disappears altogether. Ankle and trunk muscles show similar patterns of adaptation. (Adapted, with permission, from Horak and Nashner 1986.)

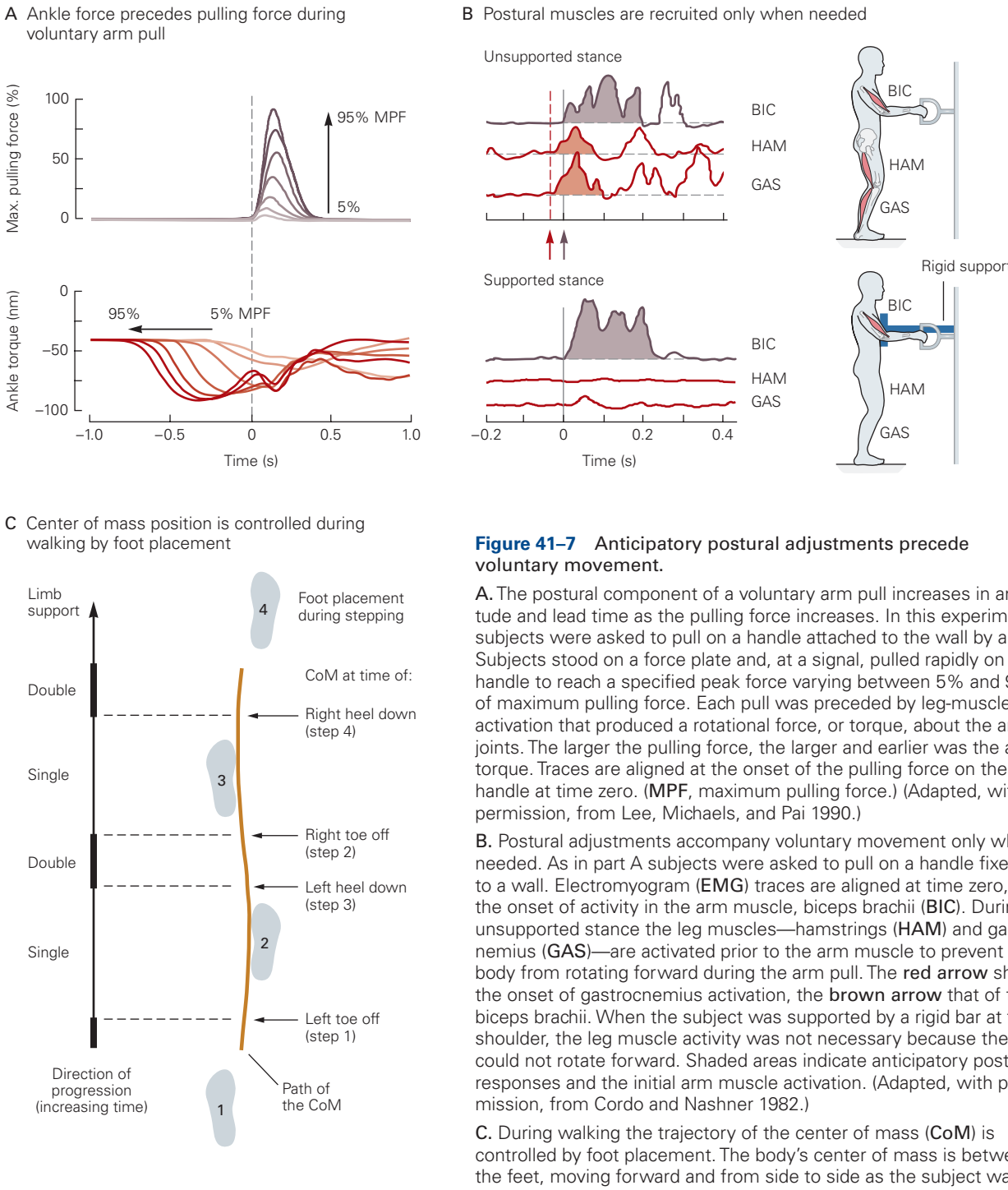
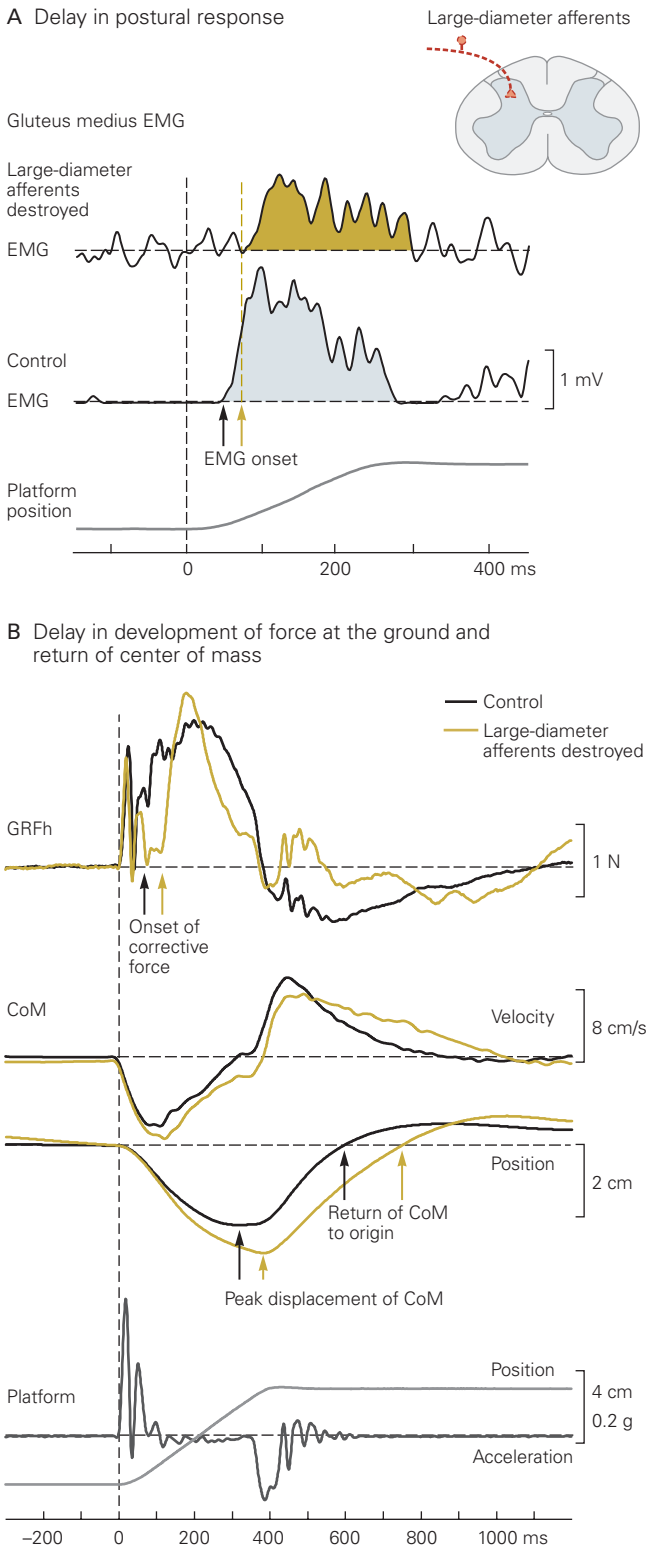


Figure 41–7 Anticipatory postural adjustments precede voluntary movement.

A. The postural component of a voluntary arm pull increases in amplitude and lead time as the pulling force increases. In this experiment subjects were asked to pull on a handle attached to the wall by a wire. Subjects stood on a force plate and, at a signal, pulled rapidly on the handle to reach a specified peak force varying between 5% and 95% of maximum pulling force. Each pull was preceded by leg-muscle activation that produced a rotational force, or torque, about the ankle joints. The larger the pulling force, the larger and earlier was the ankle torque. Traces are aligned at the onset of the pulling force on the handle at time zero. (**MPF**, maximum pulling force.) (Adapted, with permission, from Lee, Michaels, and Pai 1990.)

B. Postural adjustments accompany voluntary movement only when needed. As in part A subjects were asked to pull on a handle fixed to a wall. Electromyogram (**EMG**) traces are aligned at time zero, the onset of activity in the arm muscle, biceps brachii (**BIC**). During unsupported stance the leg muscles—hamstrings (**HAM**) and gastrocnemius (**GAS**)—are activated prior to the arm muscle to prevent the body from rotating forward during the arm pull. The **red arrow** shows the onset of gastrocnemius activation, the **brown arrow** that of the biceps brachii. When the subject was supported by a rigid bar at the shoulder, the leg muscle activity was not necessary because the body could not rotate forward. Shaded areas indicate anticipatory postural responses and the initial arm muscle activation. (Adapted, with permission, from Cordo and Nashner 1982.)

C. During walking the trajectory of the center of mass (**CoM**) is controlled by foot placement. The body's center of mass is between the feet, moving forward and from side to side as the subject walks forward. When the body is supported by only one leg, the center of mass is outside the base of support and moves toward the lifting limb. People do not fall while walking because the placement of the foot on the next step decelerates the center of mass and propels it back toward the midline. (Adapted, with permission, from MacKinnon and Winter 1993.)



The largest and most rapidly conducting sensory fibers are the Ia afferents from muscle spindles and Ib afferents from Golgi tendon organs as well as some fibers from cutaneous mechanoreceptors (see Chapter 22). Group I fibers provide rapid information about the biomechanics of the body including responses to muscle stretch, muscle force, and directionally specific pressure on the foot soles. Although group II fibers from muscle spindles and cutaneous receptors may also play a role in shaping automatic postural responses, they may be too slow to generate the earliest part of the response.

Lena Ting and co-workers showed that the temporal features of postural EMG in both quadrupeds and bipeds could be explained by a linear combination of position, velocity, and acceleration of the body's center of mass with a time delay. This suggests that information about the displacement of the center of mass is used in a feedback manner to sculpt the activation of postural muscles over time. According to this model the longer latency, slower rise time, and lower amplitude of the EMG response following destruction of group I fibers reflect a loss of acceleration information such as that encoded by muscle spindle primary receptors (Figure 41–8A). Thus center of mass acceleration may be signaled mainly by group I somatosensory fibers and center of mass velocity and position in part by the slower group II fibers.

Both proprioceptive and cutaneous inputs provide cues about postural orientation. During upright stance, for example, muscles lengthen and shorten as the body sways under the force of gravity, generating proprioceptive signals related to load, muscle length,

Figure 41–8 **Loss of large-diameter somatosensory fibers delays automatic postural responses.** Electromyograms **EMG** of postural responses to horizontal motion were recorded in a cat before and after destruction of the large-diameter (group I) somatosensory fibers throughout the body by vitamin B6 intoxication. Motor neurons and muscle strength are not affected by the loss of the somatosensory fibers, but afferent information about muscle length and force is diminished. (Reproduced, with permission, from J. Macpherson.)

A. The postural response in the gluteus medius evoked by horizontal motion of the support platform is significantly delayed after B6 intoxication. This delay of approximately 20 ms induces ataxia and difficulty in maintaining balance.

B. Destruction of group I fibers delays activation of the hind limb. This delay slows the restoration of the center of mass (**CoM**) and the recovery of balance following platform displacement. The delay in onset of the horizontal component of the ground reaction force (**GRFh**) results in a greater peak displacement of the center of mass and a delay in return of the center of mass to its origin relative to the paws.

and velocity of stretch. Joint receptors may detect compressive forces on the joints, whereas cutaneous receptors in the sole of the foot respond to motion of the center of pressure and to changes in ground reaction force angle as the body sways. Pressure receptors near the kidneys may be sensitive to gravity and used by the nervous system to help detect upright or tilted postures. All of these signals contribute to the neural map of the position of body segments with respect to each other and the support surface, and may contribute to the neural computation of center of mass motion.

Vestibular Information Is Important for Balance on Unstable Surfaces and During Head Movements

The otolithic organs of the vestibular apparatus provide information about the direction of gravity, whereas the semicircular canals measure the velocity of head rotation (see Chapter 40). Vestibular information can therefore inform the nervous system about how much the body is tilted with respect to gravity as well as whether it is swaying forward, backward, or sideways.

Somatosensory and vestibular information about the gravitational angle of the body is combined to orient the body with respect to gravity and other inertial forces. To maintain balance while riding a bike in a circular path at high speed, for example, the body and bike must be oriented with respect to a combination of gravitational and centripetal forces (Figure 41–9A).

Unlike somatosensory inputs, vestibular signals are not essential for the normal timing of balance reactions. Instead they influence the directional tuning of a postural response by providing information about the orientation of the body relative to gravity. In humans and experimental animals lacking vestibular signals, the postural response to *angular* motion or tilt of the support surface is opposite to the normal response. Instead of resisting the tilt, subjects lacking vestibular signals actively push themselves downhill (Figure 41–10). In contrast, the response to *linear*

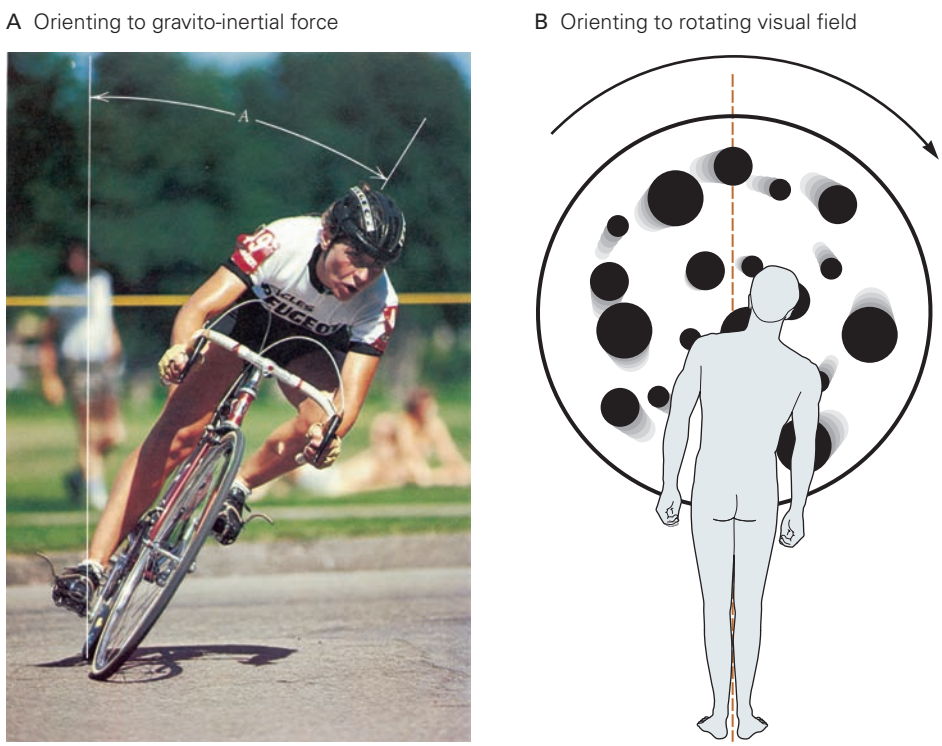


Figure 41–9 The postural system orients the body to various external reference frames.

A. When traveling at high speed along a curved path a cyclist orients to the gravito-inertial force (**angle A**), the vector sum of the force caused by gravity and the centripetal force caused by acceleration along the curved path. (Reproduced, with permission, from McMahon and Bonner 1983.)

B. The postural system can interpret rightward rotation of objects occupying a large region of the visual field as the body tilting to the left. In compensation for this illusion of motion the subject tilts to the right, adopting a new postural vertical that is driven by the visual system. Gravitational vertical is indicated by the **red dashed line**. (Adapted, with permission, from Brandt, Paulus, and Straube 1986.)

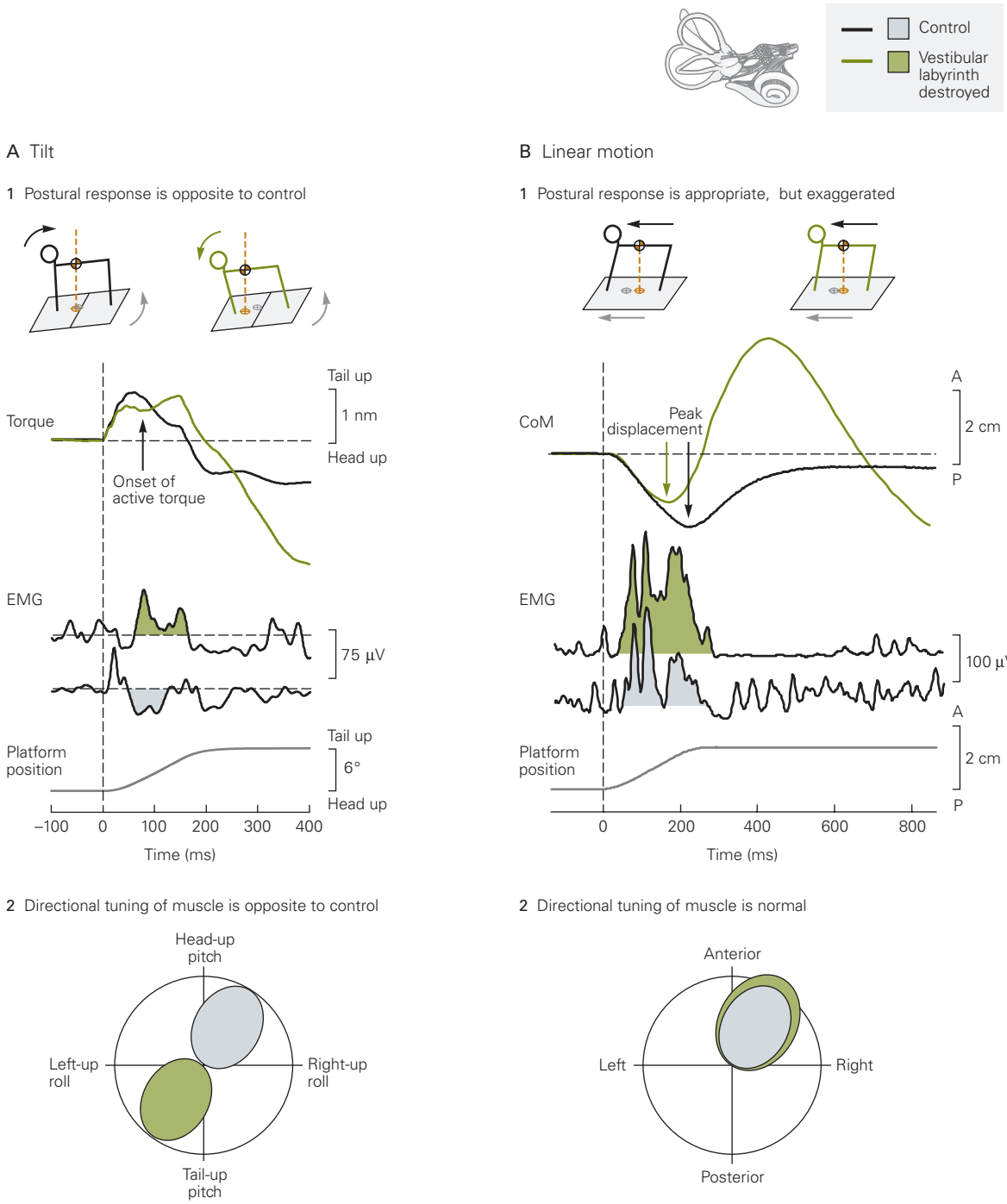


Figure 41–10 Loss of vestibular input disrupts the directional tuning of the automatic postural response to tilt of the support surface. The electromyogram (**EMG**) records are from cats standing on a movable platform before and after bilateral labyrinthectomy. (Adapted, with permission, from Macpherson et al. 2007.)

A. Without vestibular inputs the postural response to tilt of the platform is opposite to normal. **1.** The lateral gastrocnemius, an ankle extensor, is normally inhibited in response to a tail-up tilt, reducing the downhill torque (rotational force) and reducing body tilt relative to gravity. With vestibular loss the muscle is activated, which increases the downhill torque and increases body tilt, causing loss of balance. Platform displacement begins at time zero. **2.** The directional tuning of a left hip extensor muscle to platform tilt switches to the opposite quadrant after vestibular loss.

B. Immediately after vestibular loss the postural response to horizontal motion of the platform is appropriate but exceeds that of control trials. **1.** The response of the gluteus medius, a hip extensor and abductor, has normal latency but larger amplitude. In the control condition the center of mass (**CoM**) moves away from the origin and returns in a smooth trajectory. After vestibular loss the CoM displacement follows a trajectory similar to that of the control trace, but because of the larger muscle activation it peaks earlier in time. In the return phase the center of mass overshoots the origin and oscillates. Platform movement begins at time zero. (**A**, anterior; **P**, posterior.) **2.** The directional tuning of a left hip extensor muscle is the same with and without vestibular function when activated by linear motion of the platform. The amplitude of activation of the muscle is somewhat larger when vestibular function is lost.

motion of the support surface has the appropriate directional tuning and latency, even in the acute stage prior to vestibular compensation.

Why does the absence of vestibular signals cause difficulty with tilt but not with linear motion? The answer lies in how the nervous system determines the direction of vertical. Gravity is the main force that causes the body to fall. As the support surface tilts, healthy subjects orient to gravity using vestibular information to remain upright. In contrast, subjects without vestibular function use somatosensory inputs to orient themselves to the support surface and consequently fall downhill as the surface tilts. During linear motion, however, gravitational and surface vertical are collinear, and somatosensory signals are sufficient to compute the correct postural response. Although visual inputs also provide a vertical reference, visual processing is too slow to participate in the automatic postural response to rapid tilt, especially soon after the loss of vestibular function.

Without vestibular information the response to linear motion of the support surface is larger than normal (*hypermetria*), leading to overbalancing and instability (Figure 41–10B). Hypermetria is a major cause of ataxia when vestibular information is lost. Vestibular hypermetria may result from reduced cerebellar inhibition of the motor system, for the loss of vestibular inputs reduces the drive to the inhibitory Purkinje cells.

Humans and cats are quite ataxic immediately after loss of the vestibular apparatus. The head and trunk show marked instability, stance and gait are broad-based, and walking follows a weaving path with frequent falling. Instability is especially great on turning the head, probably because trunk motion cannot be distinguished from head motion using somatosensory information alone. Paul Stapley and colleagues showed that cats lacking vestibular inputs actively push themselves toward the side of a voluntary head turn, likely because somatosensory inputs that encode trunk and head motion are misinterpreted in the absence of vestibular inputs. The postural system erroneously senses that the body is falling to the side away from the head turn and generates a response in the opposite direction, resulting in imbalance.

Immediately following vestibular loss, neck muscles are abnormally activated during ordinary movements and often the head and trunk are moved together as a unit. After several months routine movement becomes more normal through vestibular compensation, which may involve greater reliance on the remaining sensory information. However, more challenging tasks are hampered by a residual hypermetria, stiffness in head-trunk control, and instability, especially when visual and somatosensory information is unavailable for postural orientation. Vestibular information is critical for balance when visual information is reduced and the support surface is not stable, for example at night, on a sandy beach, or on a boat's deck.

Visual Information Provides Advance Knowledge of Potentially Destabilizing Situations and Assists in Orienting to the Environment

Visual inputs provide the postural system with orientation and motion information from both near and far. Vision reduces body sway when standing still and provides stabilizing cues, especially when a new balancing task is attempted or balance is precarious. Skaters and dancers maintain stability while spinning by fixing their gaze on a point in the visual field. However, visual processing is too slow to significantly affect the postural response to a sudden disturbance of balance. Vision does play an important role in anticipatory postural adjustments during voluntary movements, such as planning where to place the feet when walking over obstacles.

Vision can have a powerful influence on postural orientation, as anyone can attest who has seen a movie filmed from the perspective of a moving viewer and projected on a large screen. Simulated rides in a roller coaster or plane, for example, can induce strong sensations of motion along with activation of postural muscles. An illusion of movement is induced when sufficiently large regions of the visual field are stimulated, as when a large disk in front of a standing subject is rotated. The subject responds to this illusion by tilting his body; clockwise rotation of the visual field is interpreted by the postural system as the body falling to the left, to which the subject compensates by leaning to the right (Figure 41–9B). The rate and direction of optic flow—the flow of images across the retina as people move about—provide clues about body orientation and movement.

Information from a Single Sensory Modality Can Be Ambiguous

Any one sensory modality alone may provide ambiguous information about postural orientation and body motion. The visual system, for example, cannot distinguish self-motion from object motion. We have all experienced the fleeting sensation while sitting in a stationary vehicle of not knowing whether we are moving or the adjacent vehicle is moving.

Vestibular information can also be ambiguous for two reasons. First, vestibular receptors are located in the head and therefore provide information about

acceleration of the head but not about the rest of the body. The postural control system cannot use vestibular information alone to distinguish between the head tilting on a stationary trunk and the whole body tilting by rotation at the ankles, both of which activate the semicircular canals and otolith organs. Additional information from somatosensory receptors is required to resolve this ambiguity. The otolith organs also cannot distinguish between acceleration owing to gravity and linear acceleration of the head. Tilting to the left, for example, can produce the same otolithic stimulation as acceleration of the body to the right (Figure 41–11).

Studies of vestibulo-ocular reflexes suggest there are neural circuits that can disambiguate the head-tilt component of a linear acceleration by using a combination of canal and otolith inputs. Output from this circuit may allow the postural system to determine the orientation of gravity relative to the head regardless of head position and motion. The distinction between tilt and linear motion is especially important while standing on an unstable or a tilting surface.

Somatosensory inputs may also provide ambiguous information about body orientation and motion. When we stand upright mechanoreceptors in the soles of our feet and proprioceptors in muscles and joints signal the motion of our body relative to the support surface. But somatosensory inputs alone cannot distinguish between body and surface motion, for example whether ankle flexion stems from forward body sway or tilting of the surface. Our common experience is that the ground beneath us is stable and that somatosensory inputs reflect movements of the body's center of mass as we sway. But surfaces may move relative to the earth, such as a boat's deck, or may be pliant under our weight, like a soft or spongy surface. Therefore, somatosensory information must be integrated with vestibular and visual inputs to give the nervous system an accurate picture of the stability and inclination of the support surface and of our body's relationship to earth vertical.

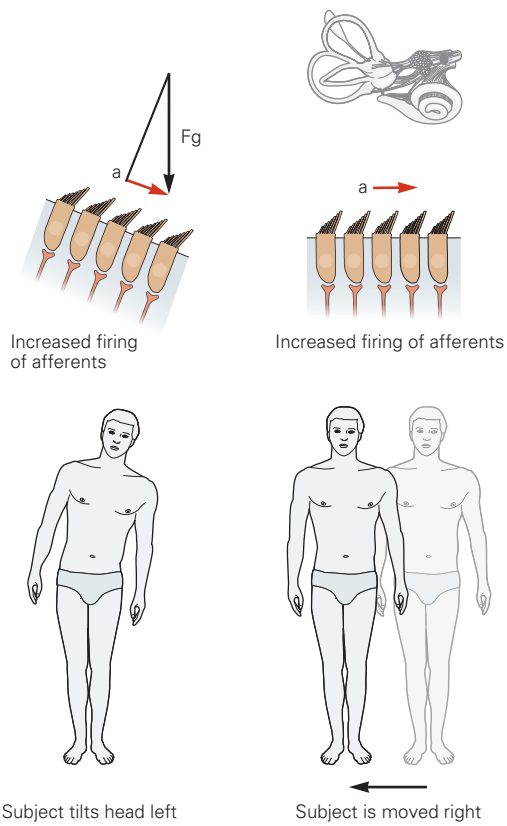


Figure 41–11 **Vestibular inputs regarding body posture and motion can be ambiguous.** The postural system cannot distinguish between tilt and linear acceleration of the body based on otolithic inputs alone. The mechanoreceptors of the vestibular system are hair bundles that bend in response to shearing forces, thus changing the firing rate of the tonically active sensory afferents. The same shearing force can result from tilting of the head (**left**), which exposes the hair cells to a portion of the acceleration (**a**) owing to gravity (**Fg**), or from horizontal linear acceleration of the body (**right**).

The Postural Control System Uses a Body Schema that Incorporates Internal Models for Balance

Because of the mechanical complexity of the body, with its many skeletal segments and muscles, the nervous system requires a coherent representation of the body and its interaction with the environment. To execute the simple movement of raising your hand and touching your nose with your index finger while your eyes are closed, your nervous system must know the characteristics (length, mass, and connections) of each segment of the arm, the shoulder, and head as well as the orientation of your arm with respect to the gravity vector and your nose. Thus information from multiple sensory systems is integrated into a central representation of the body and its environment, often called the body schema.

The body schema for postural control, as developed by Viktor Gurfinkel, is not simply a sensory map like the somatotopic representation of the skin in primary sensory cortex. Instead, it incorporates internal models of the body's relationship with the environment (see Chapter 33). This representation is used to compute appropriate anticipatory and automatic postural reactions to maintain balance and postural orientation.

A simplified example of such an internal model is one in which the body is represented as a single segment

hinged at the foot (Figure 41–12A). The internal model generates an estimate of the orientation of the foot in space, which also serves as an estimate of the orientation of the support surface, a variable that cannot be directly sensed.

Henry Head, a neurologist working in the early part of the 20th century, described the body schema as a dynamic system in which both spatial and temporal features are continually updated, a concept that remains current. To allow adequate planning of movement strategies, the body schema must incorporate not only the relationship of body segments to space and to each other but also the mass and inertia of each segment and an estimate of the external forces acting on the body including gravity.

Another component of the body schema is a model of the sensory information expected as a result of a movement. Disorientation or motion sickness may result when the actual sensory information received by the nervous system does not match the expected sensory information, as in the microgravity environment of space flight. With continued exposure to the new environment, however, the model is gradually updated until expected and actual sensory information agree and the person is no longer spatially disoriented.

The internal model for balance control must be continually updated, both in the short term, as we use experience to improve our balance strategies, and in the long term, as we age and our bodies change in shape and size. One way the body schema is updated is by changing the weighting of each of the sensory modalities.

The Influence of Each Sensory Modality on Balance and Orientation Changes According to Task Requirements

The postural control system must be able to change the relative sensitivity or weighting of different sensory modalities to accommodate changes in the environment and movement goals. Subjects on a firm, stable surface tend to rely primarily on somatosensory information for postural orientation. When the support surface is unstable subjects depend more on vestibular and visual information. However, even when the support surface is not stable, light touch with a fingertip on a stable object is more effective than vision in maintaining postural orientation and balance. Vestibular information is particularly critical when visual and somatosensory information is ambiguous or absent, such as when skiing downhill or walking below deck on a ship.

The weighting of each sensory system changes with the type of task and with the characteristics of the environment. This change can be demonstrated in an experiment in which subjects are blindfolded and asked to stand quietly on a surface that is slowly tilted by varying amounts, up to 8 degrees in magnitude. For tilts of less than 2 degrees all subjects sway with the platform, suggesting that they use somatosensory information to orient their body to the support surface. At larger tilts healthy subjects attenuate their sway and orient their posture more with respect to gravitational vertical than to the surface, as if relying more on vestibular information. In contrast, patients who have lost vestibular function persist in swaying along with the platform and subsequently fall (Figure 41–12B). This behavior accords with the patients' inappropriate automatic postural response to rapid platform tilts.

Studies such as these suggest that when people are standing on moving or unstable surfaces, the weighting of vestibular and visual information increases whereas that of somatosensory information decreases. Any sensory modality may dominate at a particular time, depending on the conditions of postural support and the specific motor behavior to be performed.

Control of Posture Is Distributed in the Nervous System

Postural orientation and balance are achieved through the dynamic and context-dependent interplay among all levels of the central nervous system, from the spinal cord to cerebral cortex.

Spinal Cord Circuits Are Sufficient for Maintaining Antigravity Support but Not Balance

Adult cats with complete spinal transection at the thoracic level can be trained to support the weight of their hindquarters with fairly normal hind limb and trunk postural orientation, but they have little control of balance. These animals do not exhibit normal postural responses in their hind limbs when the support surface moves. Their response to horizontal motion consists of small, random, and highly variable bursts of activity in extensor muscles that are considerably delayed compared to normal activity, whereas postural activity in flexor muscles is absent (Figure 41–13). Active balance is absent despite the fact that extensors and flexors can be recruited for other movements such as stepping on a treadmill.

An adult cat with a spinal transection can stand independently for only short periods of time and within a narrow range of stability; head turns in particular cause the animal to lose balance. What stability

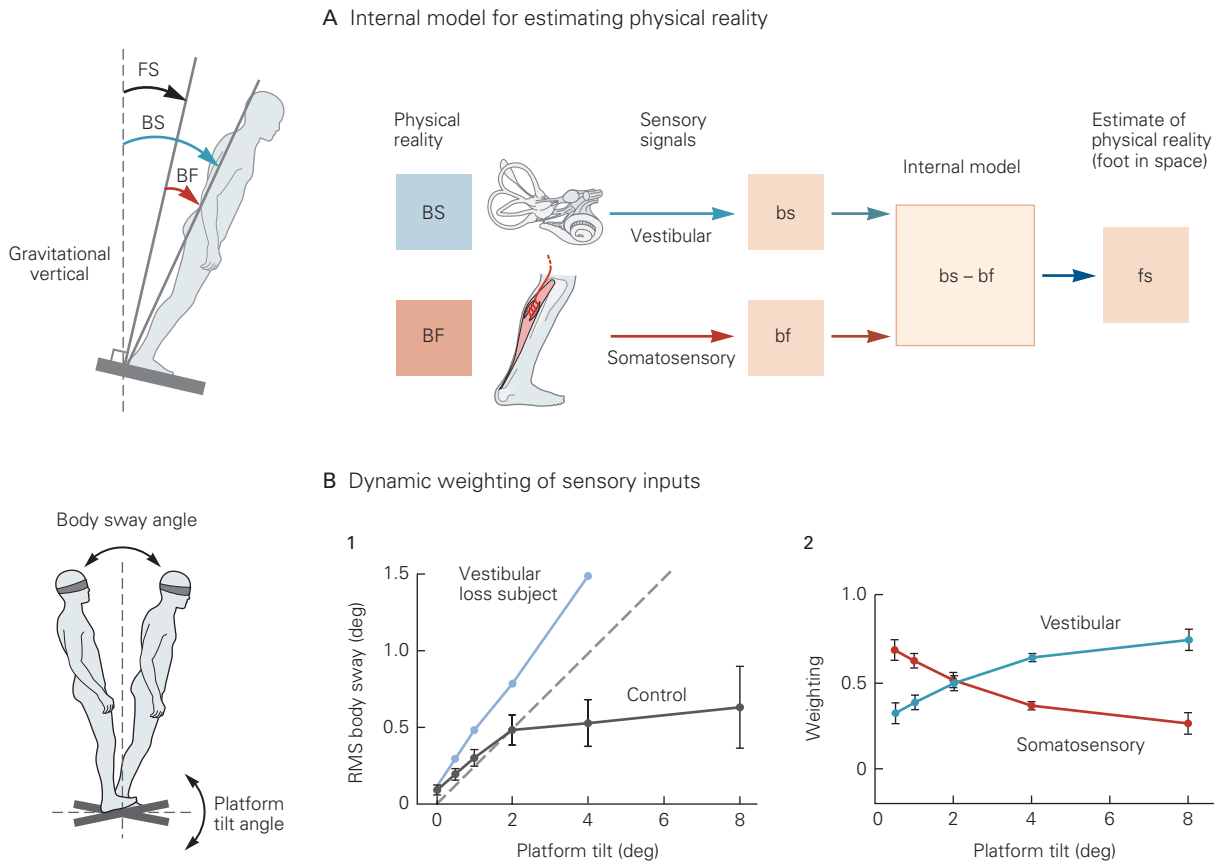


Figure 41–12 **Many types of sensory signals are integrated and weighted in an internal model that optimizes balance and orientation.** (Adapted, with permission, from Peterka 2002.)

A. The simple example of a person standing on a tilted surface illustrates how the nervous system might estimate physical variables that are not sensed directly. The physical variables are body tilt with respect to earth vertical or space (**BS**), and body angle relative to the foot (**BF**). The angle of the foot in space (**FS**) is simply the difference BS – BF. The neural estimate of body in space (**bs**) comes from vestibular and other receptors that detect tilt of the body relative to gravity. The neural estimate of body angle to foot (**bf**) comes from somatosensory signals related to ankle joint angle. The internal model for estimating physical reality, bs – bf, produces a neural estimate of the foot in space (**fs**). Such estimates of the physical world are continually updated based on experience.

B. Sensory information is weighted dynamically to maintain balance and orientation under varying conditions. The figure illustrates findings from an experiment in which human subjects stood blindfolded on a platform that slowly rotated continuously in the toes-up or toes-down direction at amplitudes of up to 8 degrees (peak to peak). **1.** Body-sway angle is measured relative to gravitational vertical during platform tilt and expressed as root mean square (**RMS**) sway in degrees. The **dashed line** represents equal platform and body sway; for example, for a platform tilt of 4 degrees an equal amount of body sway is 1 degree RMS. In control subjects the body and platform sway are equal for small platform tilts up to 2 degrees, suggesting that people normally use somatosensory signals to remain perpendicular to the platform (minimizing changes in ankle angle). With larger platform tilts, body sway does not increase much beyond 0.5 degree RMS. In contrast, subjects with vestibular loss sway even more than the platform (1.5 degrees RMS of body tilt at 4 degrees of platform tilt) and cannot remain standing at platform tilts above 4 degrees. Thus, when both vestibular and visual signals are absent, a person orients only to the support surface and has difficulty maintaining balance. **2.** In control subjects the influence of somatosensory input decreases with increasing platform tilt while the influence of vestibular input increases. At larger tilt angles the greater influence of vestibular input minimizes the degree of body sway away from gravitational vertical.

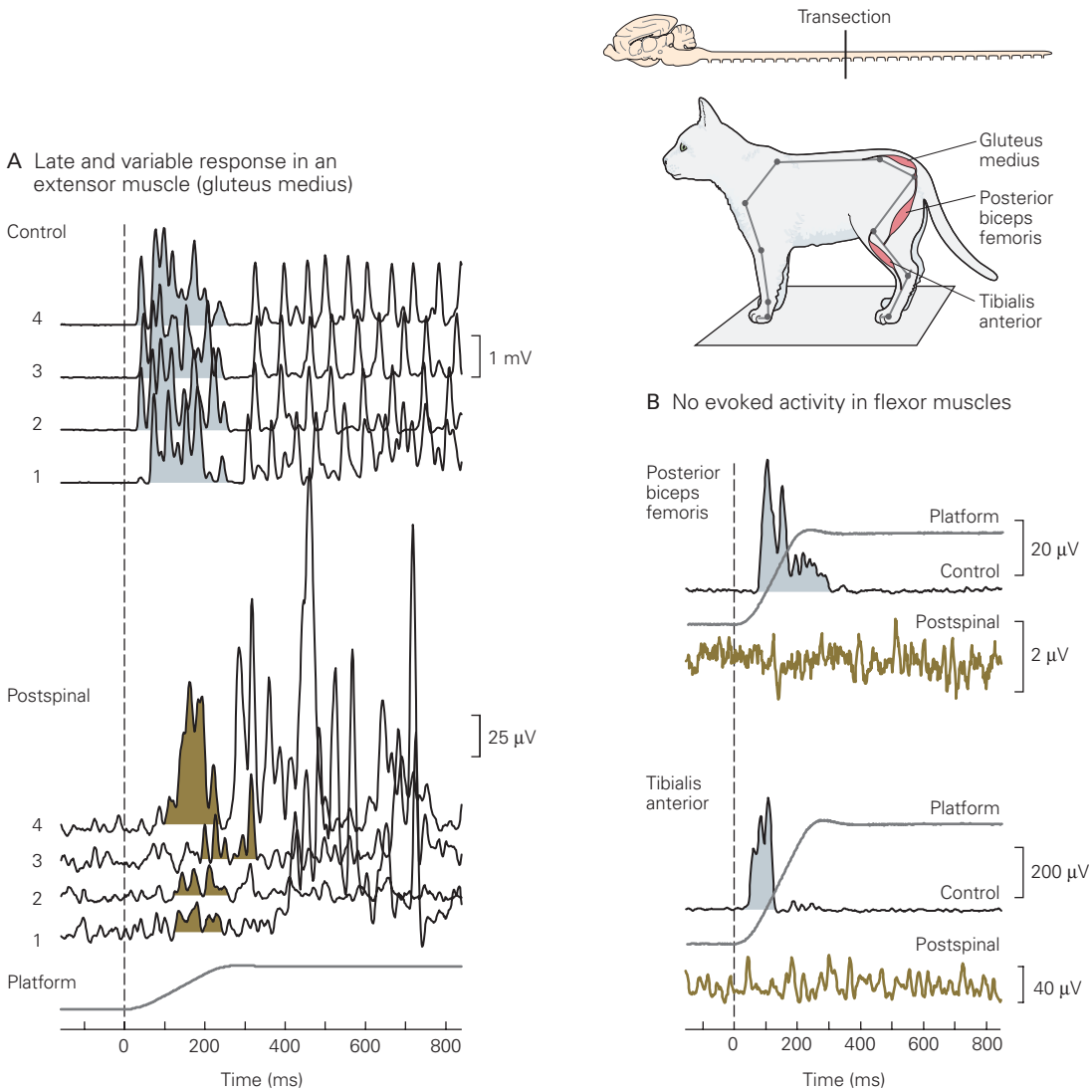


Figure 41–13 Spinal circuits alone do not generate automatic postural responses for balance. In this experiment automatic postural responses to horizontal motion are recorded before and after complete transection of the spinal cord at the level of the sixth thoracic vertebra. This transection leaves the lumbar spinal cord intact but isolated from higher neural centers. (Adapted, with permission, from Macpherson and Fung 1999.)

A. Electromyogram (EMG) records from a left hind limb extensor are disorganized after spinal transection. In four trials after transection the response amplitude of the left gluteus medius is greatly reduced following forward and rightward motion of the platform. In addition, the amplitude and onset time vary greatly between trials. Note that the scale of the postspinal records is considerably smaller than that of the control records.

B. Flexor muscles in the left hind limb are normally activated by platform motion in the backward and leftward direction. After spinal transection the flexors do not respond to translation. The posterior biceps femoris is a knee flexor; tibialis anterior is an ankle dorsiflexor.

there is likely results from the broad base of support afforded by quadrupedal stance, the stiffness of the tonically contracting hind limb extensors that support the weight of the hindquarters, and active compensation by forelimbs that continue to produce postural responses. Humans with spinal cord injuries have various amounts of antigravity muscle tonus but lack automatic postural responses below the level of the lesion. These results emphasize that antigravity support and balance control are distinct mechanisms and that the control of balance requires the involvement of supraspinal circuits.

The Brain Stem and Cerebellum Integrate Sensory Signals for Posture

If spinal circuits alone are not capable of producing automatic postural responses, what supraspinal centers are responsible for these responses? Although the answer to this question remains unknown, good candidates include the brain stem and cerebellum, which are highly interconnected and work together to modulate the descending commands to spinal motor centers of the limbs and trunk. These regions have the input-output structure that would be expected of centers for postural control.

Muscle synergies for automatic postural responses may be organized in the brain stem, perhaps the reticular formation. However, adaptation of postural synergies to changes in the environment and task demands may require cerebellar influence.

Two regions of the cerebellum influence orientation and balance: the vestibulocerebellum (nodulus, uvula, and fastigial nucleus) and the spinocerebellum (anterior lobe and interpositus nucleus). These regions are interconnected with the vestibular nuclei and reticular formation of the pons and medulla (see Figure 42–3). Lesions of the brain stem and vestibulocerebellum produce a variety of deficits in head and trunk control and a tendency to tilt from vertical, even with eyes open, suggesting a deficit in the internal representation of postural orientation. Lesions of the spinocerebellum result in excessive postural sway that is worse with the eyes closed, ataxia during walking, and hypermetric postural responses, suggesting deficits in balance reactions. Certain regions in the pons and medulla facilitate or depress extensor tonus and could thereby influence antigravity support.

The brain stem and cerebellum are sites of integration of sensory inputs, perhaps generating the internal model of body orientation and balance. Vestibular and visual inputs are distributed to brain stem centers (see Chapter 45) and the vestibulocerebellum. The spinocerebellum receives signals from rapidly conducting proprioceptive and cutaneous fibers. More slowly conducting somatosensory fibers project to the vestibular nuclei and reticular formation.

Two major descending systems carry signals from the brain stem and cerebellum to the spinal cord and could therefore trigger the automatic postural response for balance and orientation. The medial and lateral vestibulospinal tracts originate from the vestibular nuclei, and the medial and lateral reticulospinal tracts originate from the reticular formation of the pons and medulla (see Figure 42–7). Lesions of these tracts result in profound ataxia and postural instability. In contrast, lesions of the corticospinal and rubrospinal tracts have minimal effect on balance even though they produce profound disturbance of voluntary limb movements.

The Spinocerebellum and Basal Ganglia Are Important in Adaptation of Posture

Patients with spinocerebellar disorders, such as alcoholic anterior-lobe syndrome, and basal-ganglion deficits, such as Parkinson disease, experience postural difficulties. This suggests that the spinocerebellum and basal ganglia play complementary roles in adapting postural responses to changing conditions.

The spinocerebellum is where the magnitude of postural responses is adapted based on experience. The basal ganglia are important for quickly adjusting the postural set when conditions suddenly change, to ensure that postural responses are approximately correct. Both the spinocerebellum and the basal ganglia regulate muscle tone and force for voluntary postural adjustments. They are not necessary, however, for triggering or constructing the basic postural patterns.

Patients with disorders of the spinocerebellum have difficulty adjusting the magnitude of balance adjustments over the course of repeated trials but can readily adapt postural responses immediately after a change in conditions. For example, a patient standing on a movable platform exhibits appropriate postural responses when platform velocity is increased with each trial. These postural adjustments rely on velocity information, which is encoded by somatosensory inputs at the beginning of platform movement.

In contrast, when the amplitude of platform movement can be predicted on the basis of repeated presentation, a patient is unable to adjust the amplitude of his response to that of the anticipated perturbation. Because the amplitude of platform movement is not known until the platform has stopped moving, well after the initial postural response is complete, a subject must use his experience from one trial to modify his response in a subsequent trial of the same amplitude. Whereas a healthy subject does this quite readily, a patient with spinocerebellar disorders is unable to efficiently adapt his postural responses based on recent experience (Figure 41–14A).

In a healthy subject muscle activity during sudden backward motion of the support surface is appropriately scaled to counteract the forward sway induced by the perturbation. A subject with spinocerebellar disease always over-responds, although the timing of muscle activation is normal (Figure 41–14B). As a result, this individual returns beyond the upright

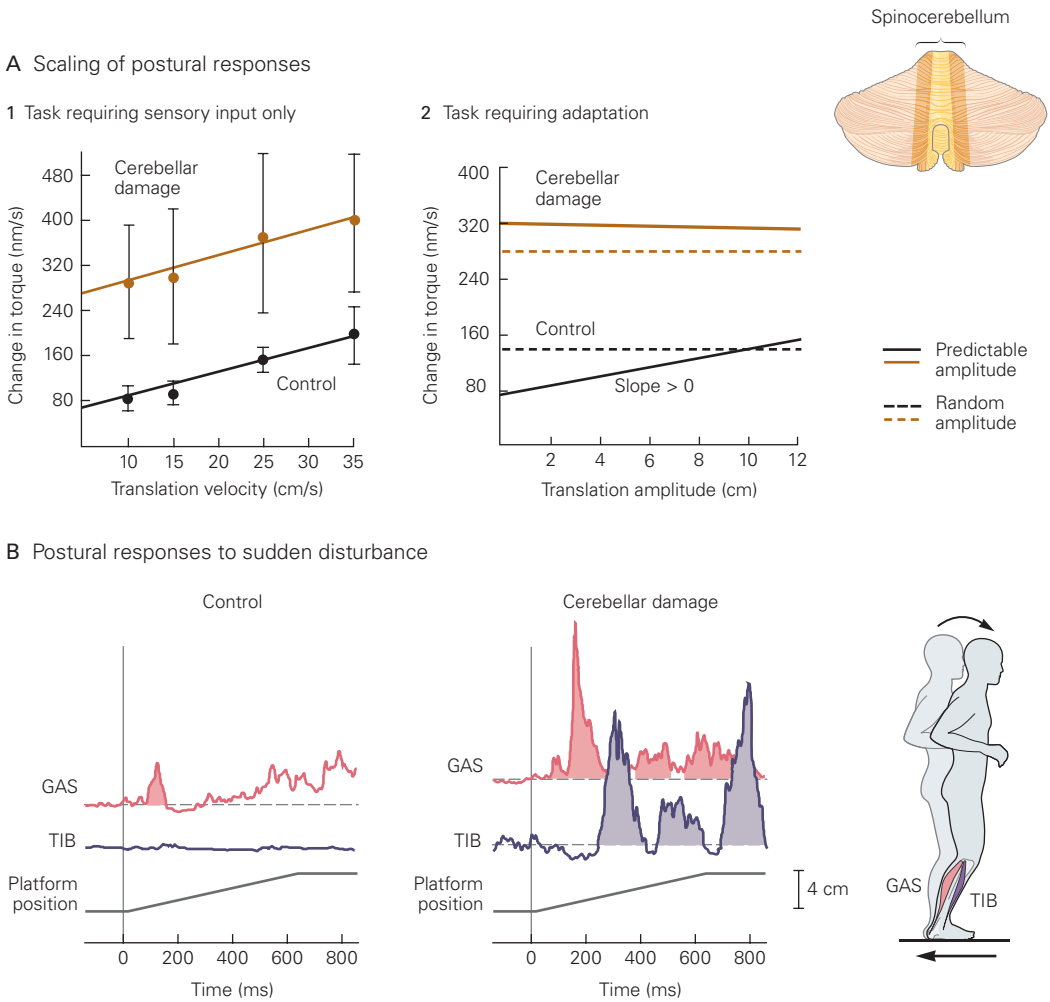


Figure 41–14 The spinocerebellum has a role in adapting postural responses to changing conditions. The spinocerebellum is important for adapting postural responses based on experience. Patients with a spinocerebellar disorder can use immediate sensory input but not experience to adjust automatic postural responses. (Adapted, with permission, from Horak and Diener 1994.)

A. 1. A subject stands on a platform that is moved horizontally; the velocity is increased on each trial. Maintaining balance requires scaling responses to the velocity of the platform using sensory feedback. The adjustments in a subject with a spinocerebellar disorder have the same regression coefficient (slope) as those of a control subject, even though in each trial the responses are larger and more variable than those of the control subject. **2.** When subjects are required to anticipate and adapt to platform translation, the postural adjustments in the spinocerebellar subject are compromised. When translation amplitude is random, responses are large, as if the subject expected a large translation. When trials with the same amplitude are repeated, a control subject learns to predict the amplitude of the disturbance and adjust his response. In contrast, a spinocerebellar subject shows no improvement in performance; he cannot use his experience in one trial to adjust his responses in subsequent trials. The responses are large, as if the subject always expected the large translation.

B. Postural responses to sudden disturbances are hypermetric in spinocerebellar patients. In this experiment subjects stand on a platform that is moved backward (6 cm amplitude at 10 cm/s). In a control subject the onset of movement evokes a small burst of activity in the gastrocnemius (**GAS**), an ankle extensor. In a subject with damage to the anterior lobe of the cerebellum the muscle responses are overly large, with bursts of activity alternating between the gastrocnemius and its antagonist, the tibialis anterior (**TIB**).

position and oscillates back and forth. Reminiscent of the hypermetria observed immediately after labyrinthectomy, cerebellar hypermetria may also result from loss of Purkinje-cell inhibition on spinal motor centers.

A patient with Parkinson disease can, with sufficient practice, gradually modify his postural responses but has difficulty changing responses when conditions change suddenly. Such postural inflexibility is seen when initial posture changes. For example, when a normal subject on a movable platform switches from standing upright to sitting on a stool, the pattern of his automatic postural response to backward movement of the platform changes immediately. Because leg-muscle activity is no longer necessary after the switch from standing to sitting, this component ceases to be recruited.

In contrast, a patient with Parkinson disease employs the same muscle activation pattern for both sitting and standing (Figure 41–15). L-DOPA replacement therapy does not improve the patient's ability to switch postural set. With repetition of trials in the seated posture, however, the leg-muscle activity eventually disappears, showing that enough experience permits adaptation of postural responses. A patient with Parkinson disease also has difficulty when instructed to increase or decrease the magnitude of a postural response, a difficulty that is consistent with the inability to change cognitive sets quickly.

A patient with a basal ganglion disorder has problems with postural tone and force generation in addition to an inability to adapt to changing conditions. The bradykinesia (slowness of movement) of Parkinson disease is reflected in slow development of force in postural responses and the disease's rigidity is manifested in co-contraction and stiffness. L-DOPA replacement greatly improves a patient's ability to generate not only forceful voluntary movements but also the accompanying postural adjustments, such as rising onto the toes and gait. However, neither the automatic postural response to an unexpected disturbance nor postural adaptation is improved by L-DOPA, suggesting that these functions involve the nondopaminergic pathways affected by Parkinson disease.

Cerebral Cortex Centers Contribute to Postural Control

Centers in the cerebral cortex influence postural orientation and equilibrium, including both anticipatory and automatic postural responses. Most voluntary movements, which are initiated in the cerebral cortex, require postural adjustments that must be integrated with the primary goal of the movement in both timing and amplitude. Where this integration occurs is not clear.

The cerebral cortex has more control over anticipatory postural adjustments than automatic postural reactions. However, recent electroencephalographic (EEG) studies show that areas of cerebral cortex are activated by anticipation of a postural disturbance before an automatic postural response is initiated. This finding is consistent with the idea that the cortex optimizes balance control as part of motor planning.

The supplementary motor area and temporoparietal cortex have both been implicated in postural control. The supplementary motor area (see Chapter 38) is likely involved with anticipatory postural adjustments that accompany voluntary movements. The temporoparietal cortex appears to integrate sensory information and may contain internal models for perception of body verticality. Lesions of insular cortex can impair perception of the visual vertical whereas lesions of superior parietal cortex impair perception of postural vertical, and either of these defects may impair balance when standing on an unstable support.

Sensorimotor cortex receives somatosensory inputs signaling balance disturbances and postural responses. However, this region is not essential for automatic postural adjustments. Jean Massion and colleagues have shown that lesioning the motor cortex in cats impairs the lifting of the forelimb evoked by light touch during stance, but does not abolish the accompanying postural adjustment in the contralateral forelimb. Although the sensorimotor cortex is not responsible for postural adjustments, it may have a role in the process.

Behavioral studies, too, have implicated cortical processes in postural control. Control of posture, like control of voluntary movement, requires attention. When subjects must press a button following a visual or auditory cue while also maintaining balance, their reaction time increases with the difficulty of the task (balancing on one foot versus sitting, for example). Moreover, when subjects try to perform a cognitive task while actively maintaining posture, the performance of either or both can degrade. For example, when a subject is asked to count backward by threes while standing on one foot, both the cognitive task and postural adjustment deteriorate. The timing of automatic postural responses to unexpected disturbances is little affected by cognitive interference.

Balance control is also influenced by emotional state, thus implicating the limbic system in posture control. Fear of falling, for example, can increase postural tone and stiffness, reduce sway area, increase sway velocity, and alter balancing strategies in response to disturbances.

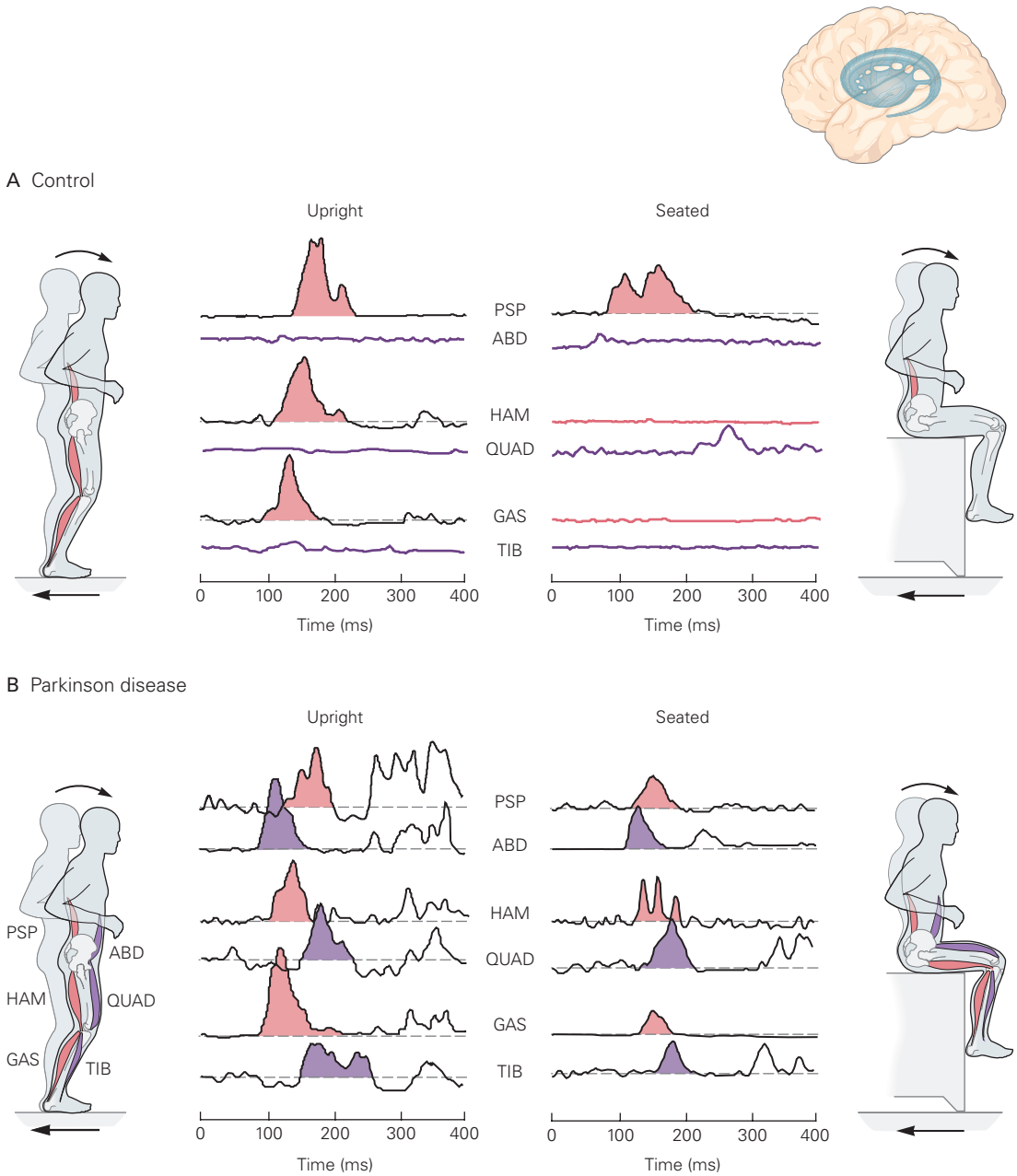


Figure 41–15 The basal ganglia are important for adapting postural responses to a sudden change in initial conditions. (Adapted, with permission, from Horak, Nutt, and Nashner 1992.)

A. When a normal subject switches from upright stance to sitting he immediately modifies his response to backward movement of the support platform. The postural response to movement while seated does not involve the leg muscles—the gastrocnemius (**GAS**) and hamstrings (**HAM**)—but does activate the paraspinal muscles (**PSP**) and with shorter latency than in the response to movement while standing. (**ABD**, abdominals; **QUAD**, quadriceps; **TIB**, tibialis anterior.)

B. A patient with Parkinson disease does not suppress the leg-muscle response in the first trial after switching from standing to sitting. The postural response of this subject is similar for both initial positions: antagonist muscles (**purple**) are activated along with agonists (**pink**).

Although the roles of specific areas of cerebral cortex in postural control are largely undefined, there is no doubt that the cortex is important for learning new, complex postural strategies. The cortex must be involved in the amazing improvement in balance and postural orientation of athletes and dancers who use cognitive information and advice from coaches. In fact, the cerebral cortex is involved in postural control each time we consciously maintain our balance while walking across a slippery floor, standing on a moving bus, or waiting tables on a rocking ship.

An Overall View

Although we are usually unaware of it, the posture control system is active during most of the activities we perform daily. Automatic postural adjustments prevent falling when some external force disrupts our balance. These responses are not simple reflexes but are highly organized, flexible, and adaptive patterns of muscle activation. Anticipatory postural adjustments accompany our voluntary movements to maintain balance and orientation.

Somatosensory, vestibular, and visual inputs all contribute to postural control for balance and orientation with differing degrees of influence as our environment changes. Many areas of the nervous system integrate sensory inputs to form a unified representation of the body's orientation and motion and of the environment. This body schema is used to compute the appropriate postural adjustments to maintain balance.

The postural system is highly adaptive, both in the short term to optimize postural behavior to a continually changing environment, and in the long term to accommodate changes in body morphology and mechanics caused by growth and development, aging, disease, and injury.

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Fay B. Horak

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