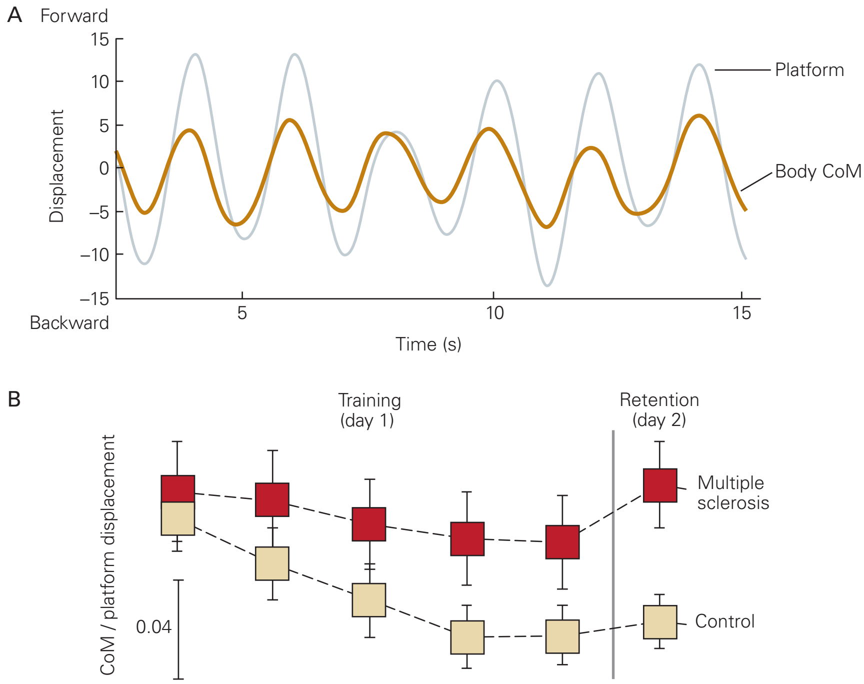


Figure 36–7 **Postural responses can be learned and retained with practice.**

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

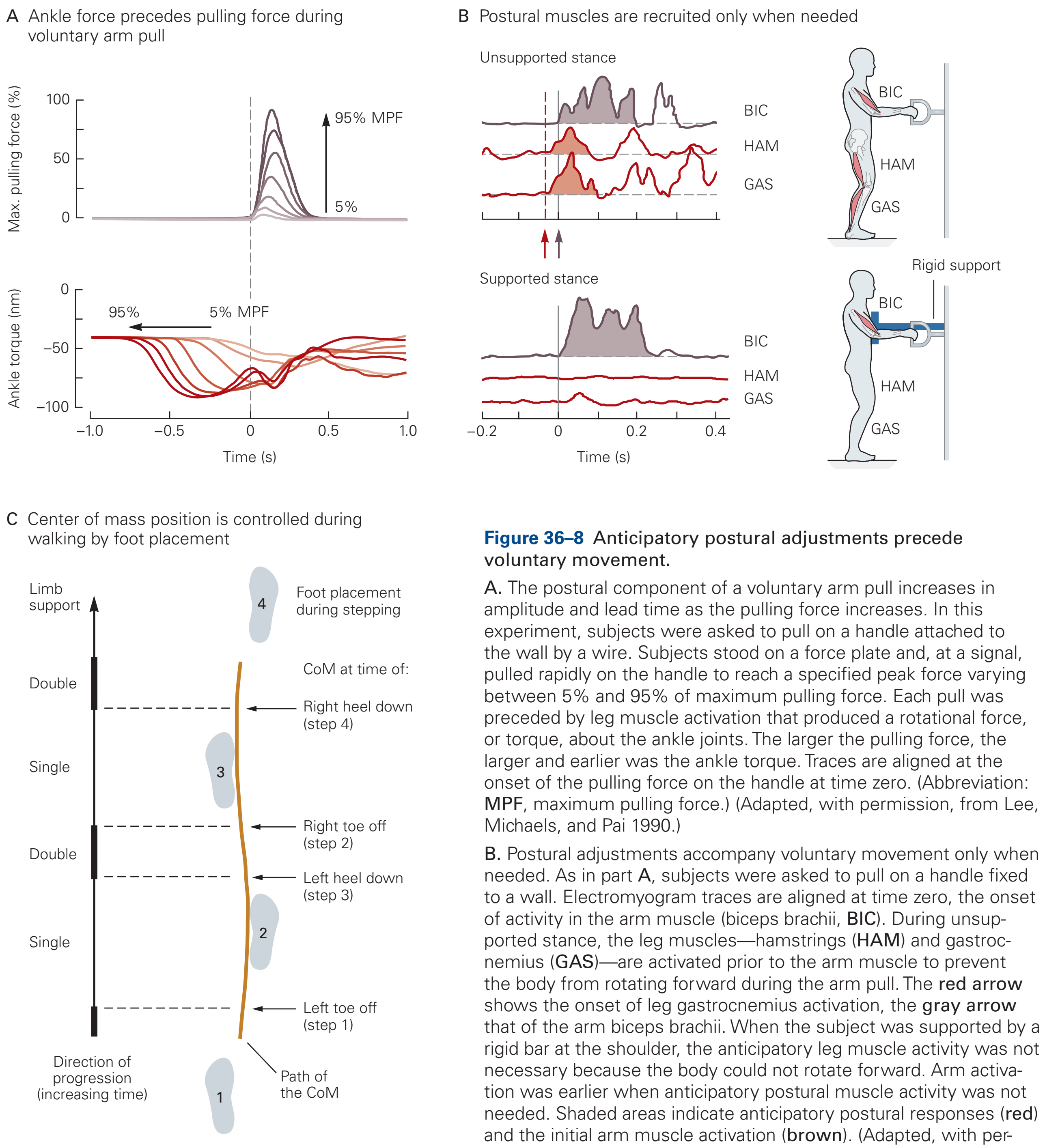


Figure 36–8 **Anticipatory postural adjustments precede voluntary movement.**

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. (Abbreviation: **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 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 leg gastrocnemius activation, the **gray arrow** that of the arm biceps brachii. When the subject was supported by a rigid bar at the shoulder, the anticipatory leg muscle activity was not necessary because the body could not rotate forward. Arm activation was earlier when anticipatory postural muscle activity was not needed. Shaded areas indicate anticipatory postural responses (**red**) and the initial arm muscle activation (**brown**). (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 (single support phase), the CoM 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 CoM and propels it back toward the midline. (Adapted from MacKinnon and Winter 1993.)

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 voluntary movements, postural adjustments control the body's angular momentum by anticipating rotational forces.

Posture Control Is Integrated With Locomotion

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 (Figure 36–8C). During walking, the center of mass is within the base of support only when both feet are on the ground, the double stance phase, which is only one-third of a gait cycle. 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 placement of each step to control the speed and trajectory of the center of mass. The nervous system plans foot placement several steps in advance using visual information about the terrain and surrounding environment.

The main postural challenge during walking is controlling the center of mass of the upper body over the moving legs, especially in the lateral direction. Excessive lateral displacement of the trunk and excessive lateral foot placement variability are signs of postural instability during locomotion. Patients with abnormal postural stability during gait may nevertheless exhibit normal automatic and anticipatory postural adjustments, postural sway in stance under different sensory conditions, and orientation to vertical, suggesting that postural control and gait have different nervous system circuits.

Somatosensory, Vestibular, and Visual Information Must Be Integrated and Interpreted to Maintain Posture

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

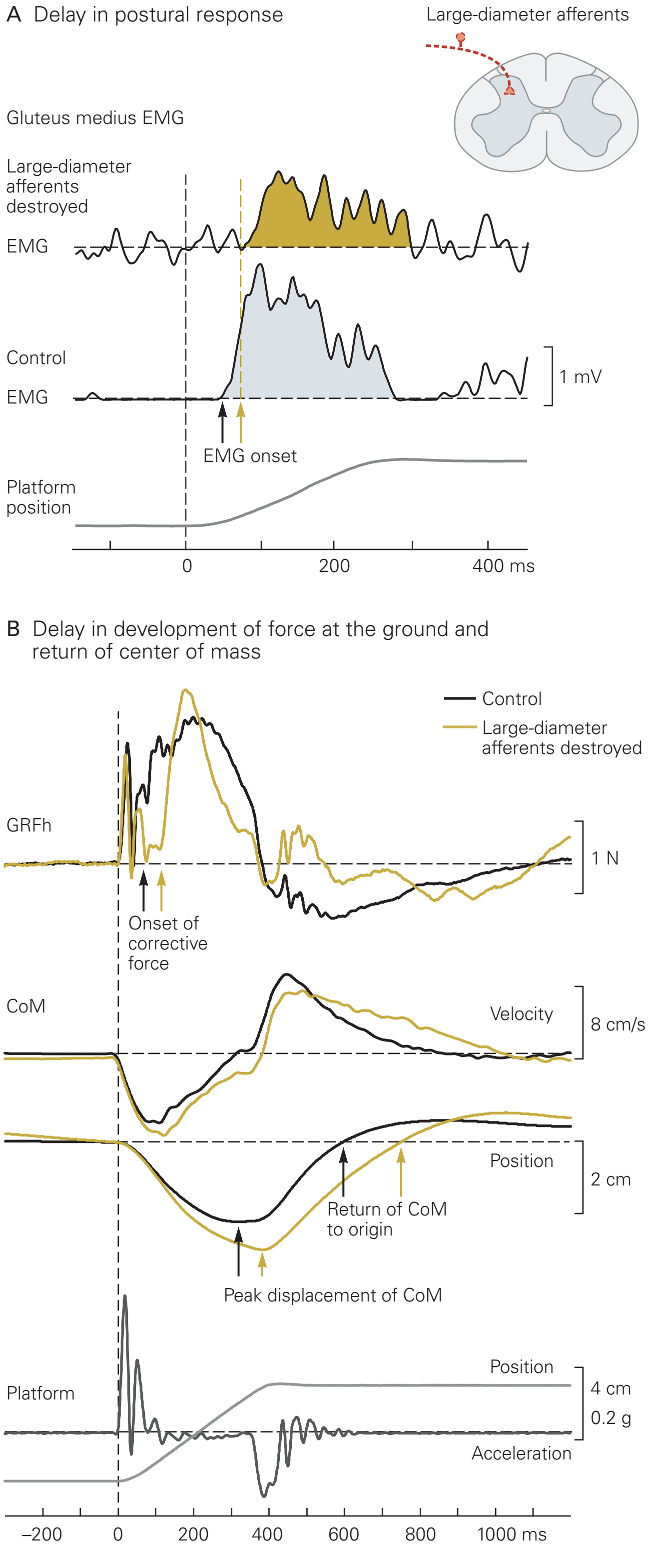
According to prevailing theory, sensory modalities are integrated to form an internal representation of the body housed within the parietal cortex that the nervous system uses to plan and execute motor behaviors. Over time, this internal representation must adapt to changes associated with early development,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

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

Many types of somatosensory fibers trigger and shape the automatic postural response. The largest fibers, those in group I (12–20 μm in diameter), appear to be essential for normal response latencies. The longer latency, slower rise time, and lower amplitude of the EMG response following destruction of the group I fibers reflect a loss of acceleration information encoded by muscle spindle primary receptors (Figure 36–9A). 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 (Chapter 18). 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. However, group II fibers from muscle spindles and cutaneous receptors may also play a role in shaping automatic postural responses. Although they may be too slow to generate the earliest part of the response, they likely encode center of mass velocity and position.

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, 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 are sensitive to gravity (somatic graviception) and are 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 platform surface and may contribute to the neural computation of center of mass motion.

The large-diameter, fast somatosensory fibers from muscle spindles are critical for maintaining balance during stance. When these axons die, as occurs in some forms of peripheral neuropathy, automatic postural responses to movement of a platform 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 36–9). 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. Accordingly, individuals with large-fiber peripheral neuropathy in the legs experience ataxia and difficulties with balance.

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 (Chapter 27). Vestibular information thus informs 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 36–10A).

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 functional vestibular afferent pathways, the postural response to *angular* motion or tilt of the support surface is opposite to the

Figure 36–9 (Left) **Loss of large-diameter somatosensory fibers delays automatic postural responses.** Electromyograms (**EMGs**) of postural responses to horizontal motion of a moveable platform were recorded in a cat before and after destruction of the large-diameter (group I) somatosensory fibers throughout the body by vitamin B_6 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 destruction of group I fibers. 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 CoM and a delay in its return to its origin relative to the paws.

A Orienting to gravito-inertial force

B Orienting to rotating visual field

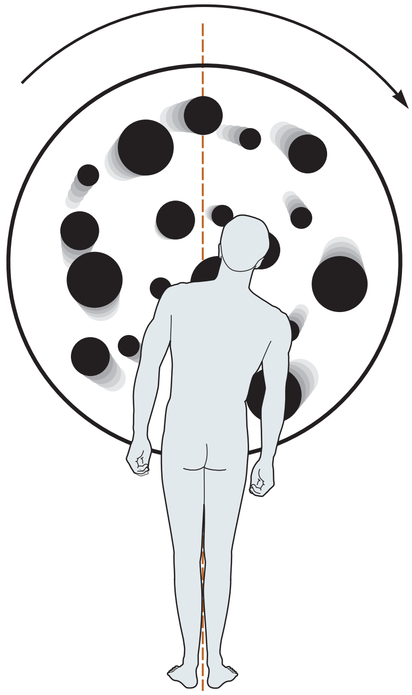


Figure 36–10 The postural system orients the body to various external reference frames.

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. (Used, with permission, from Joseph Daniel, Story Arts Media, LLC. Previously published in 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 orientation that is driven by the visual system. The **red dashed line** indicates gravitational vertical. (Adapted, with permission, from Brandt, Paulus, and Straube 1986.)

normal response. Rather than resisting the tilt, subjects lacking vestibular signals do the opposite and accentuate the tilt through their own muscular activity. In contrast, the response to horizontal translation motion of a platform 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. 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. Cats and humans lacking vestibular inputs produce motor output that results in them actively pushing 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 tilt 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 deck.

Visual Inputs Provide the Postural System With Orientation and Motion Information

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 and unexpected 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, evident when watching a movie scene filmed from the perspective of a moving viewer and projected on a large screen. Simulated rides in a roller coaster or airplane 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 36–10B). 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 36–11).

Studies suggest that 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.

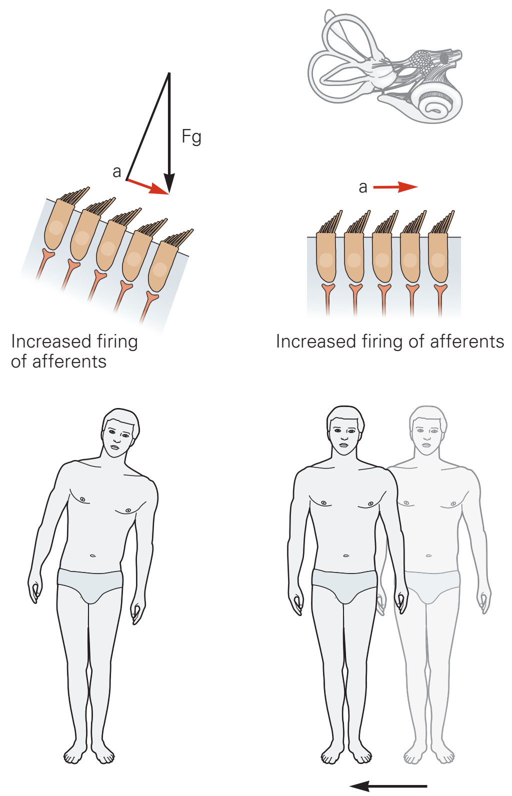


Figure 36–11 Vestibular inputs regarding body posture and motion can be ambiguous. The postural system cannot distinguish between tilt and linear acceleration of the body based on otolith inputs alone. The mechanoreceptors of the vestibular system are hair bundles that bend in response to shearing forces, 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 detailed 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, 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. The body schema 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 36–12A). 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.

The body schema integrates sensory information from the somatosensory, vestibular, and visual systems to orient the body to vertical. Even in the dark, people can accurately reorient a projected line to a vertical position (visual vertical) and they can reorient themselves to vertical when sitting on a tilting swing (gravitational vertical). Visual vertical and gravitational vertical are independent of each other. Patients with asymmetrical vestibular function show abnormal visual vertical but normal gravitational vertical, whereas patients with hemi-neglect from stroke show abnormal gravitational vertical but normal visual vertical.

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 relative sensitivity or weighting of each sensory system.

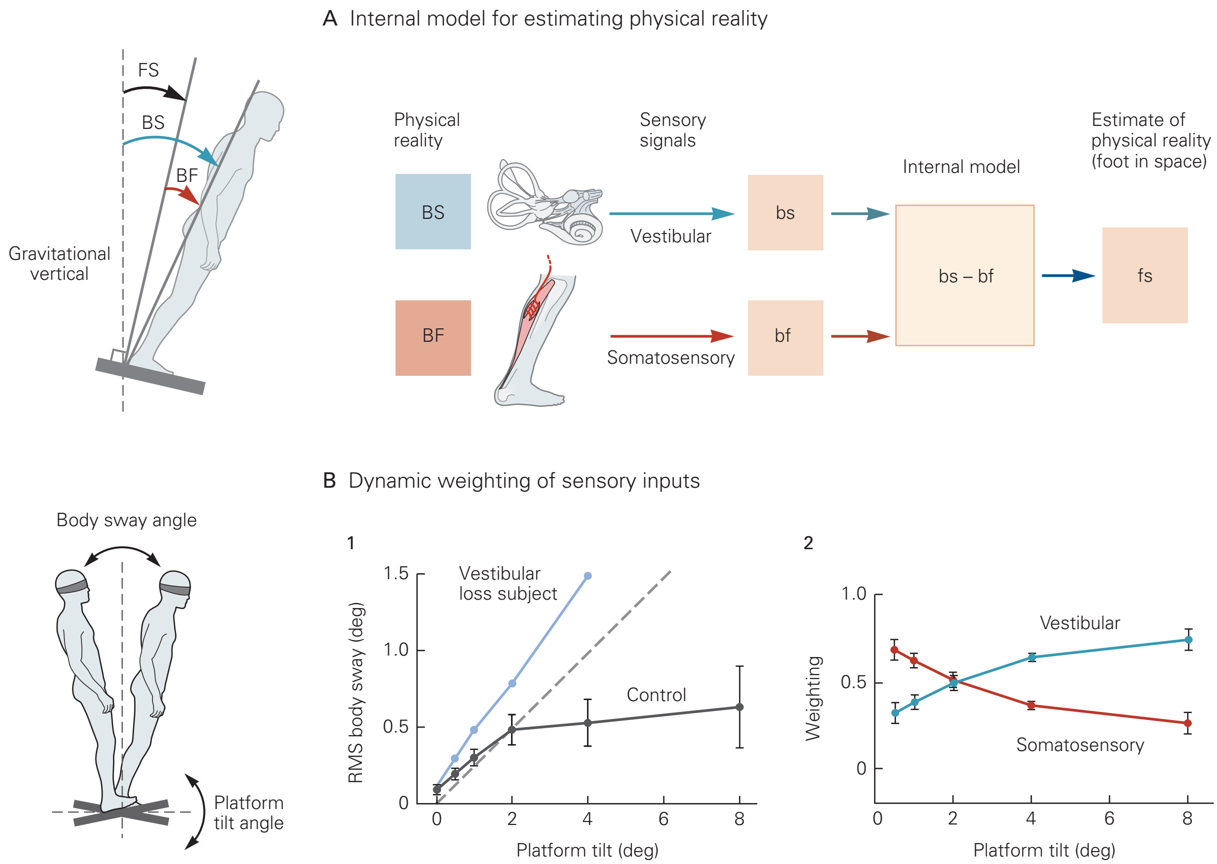


Figure 36–12 Many types of sensory signals are integrated and weighted in an internal model that optimizes balance and orientation. (Adapted from Peterka 2002.)

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 body-in-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° (peak to peak). **1.** Comparison of body sway during surface oscillations in a subject with loss of vestibular function and a group of control subjects. 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°, an equal amount of body sway is 1° RMS. In control subjects, the body and platform sway are equal for small platform tilts up to 2°, 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° RMS. In contrast, subjects with vestibular loss sway even more than the platform (1.5° RMS of body tilt at 4° of platform tilt) and cannot remain standing at platform tilts above 4°. Thus, when both vestibular and visual signals are absent, a person attempts to maintain his position only relative to the support surface and has difficulty maintaining balance as that surface moves. **2.** In control subjects, as platform tilt increases, 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.

Control of Posture Is Task Dependent

The senses and muscles used to control posture vary, depending on task constraints and requirements. For example, when vestibular and somatosensory information is altered while working on a space station, vision is used to orient the body to tasks, and the goal of postural equilibrium changes from preventing falls due to gravity to preventing unintended collision with objects due to inertia. A healthy nervous system very quickly adapts to changing tasks, goals, and environments by modifying its relative dependence upon different sensory information and by using different sets of muscles to optimize achieving the goals of both posture control and voluntary movements.

Task Requirements Determine the Role of Each Sensory System in Postural Equilibrium and Orientation

The postural control system must be able to change the weighting of different sensory modalities to accommodate changes in the environment and movement goals. Subjects standing 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 changeable weighting of individual sensory modalities was demonstrated in an experiment in which subjects were blindfolded and asked to stand quietly on a surface with a tilt that slowly oscillated by varying amounts, up to 8° in magnitude. For tilts of less than 2°, all subjects sway with the platform, suggesting that they use somatosensory information to orient their body to the support surface (Figure 36–12B). At larger tilts, healthy subjects attenuate their sway and orient their posture more with respect to gravitational vertical than to the surface, as they rely more on vestibular information so they stop increasing body sway. Thus, relative sensory weighting changes in control subjects such that somatosensory weight is highest with a stable platform and vestibular weight is highest when standing on an unstable surface, such as with large surface tilts (Figure 36–12B2). In contrast, patients who have lost vestibular function persist in swaying along with the platform and subsequently fall during large surface tilts. This behavior is consistent with the patients' inappropriate automatic postural response to 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. The major areas of the brain involved in postural control are shown in Figure 36–13. Signals from specific areas in all lobes of the cerebral cortex converge and are integrated to determine appropriate outputs from motor cortical areas to subcortical structures. The basal ganglia, cerebellum, and pedunculopontine nucleus then send outputs to the brain stem. Ultimately, inputs from these varied sources result in activation of the reticulospinal and vestibulospinal pathways, which descend to the spinal cord where they contact interneurons and spinal motor neurons for postural control.

Afferent inputs from visual, vestibular, and somatosensory sources are integrated along the neuraxis, including the vestibular nuclei and right parietal cortex, to inform the internal model of body orientation and balance. This internal model is continually updated by the cerebellum based on error signals between expected and actual sensory feedback following motor commands.

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

Adult cats with complete spinal transection at the thoracic level can, with experience, 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, and postural activity in flexor muscles is completely absent. Active balance is absent despite the fact that extensors and flexors can