Excitatory-Inhibitory Antagonism Between Pontine and Medullary Reticular Nuclei

The reticular nuclei are divided into two major groups: (1) *pontine reticular nuclei,* located slightly posteriorly and laterally in the pons and extending into the mesencephalon, and (2) *medullary reticular nuclei,* which extend through the entire medulla, lying ventrally and medially near the midline. These two sets of nuclei function mainly antagonistically to each other, with the pontine exciting the antigravity muscles and the medullary relaxing these same muscles.

Pontine Reticular System. The pontine reticular nuclei transmit excitatory signals downward into the cord through the *pontine reticulospinal tract* in the anterior column of the cord, as shown in Figure 55–8. The fibers of this pathway terminate on the medial anterior motor neurons that excite the axial muscles of the body, which support the body against gravity—that is, the muscles of the vertebral column and the extensor muscles of the limbs.

The pontine reticular nuclei have a high degree of natural excitability. In addition, they receive strong excitatory signals from the vestibular nuclei, as well as from deep nuclei of the cerebellum. Therefore, when the pontine reticular excitatory system is unopposed by the medullary reticular system, it causes powerful excitation of antigravity muscles throughout the body, so much so that four-legged animals can be placed in a standing position, supporting the body against gravity without any signals from higher levels of the brain.

Medullary Reticular System. The medullary reticular nuclei transmit *inhibitory* signals to the same antigravity anterior motor neurons by way of a different tract, the *medullary reticulospinal tract,* located in the lateral column of the cord, as also shown in Figure 55–8. The medullary reticular nuclei receive strong input collaterals from (1) the corticospinal tract, (2) the rubrospinal tract, and (3) other motor pathways. These normally activate the medullary reticular inhibitory system to counterbalance the excitatory signals from the pontine reticular system, so that under normal conditions, the body muscles are not abnormally tense.

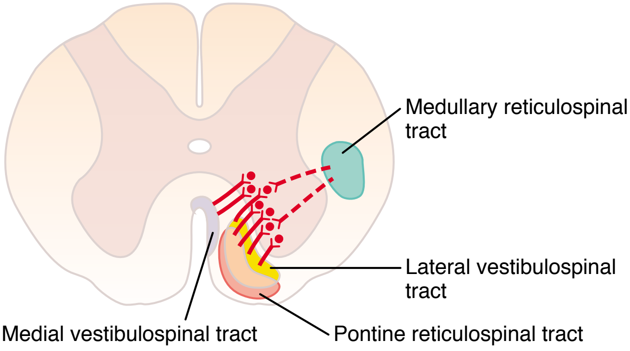


Figure 55–8

Vestibulospinal and reticulospinal tracts descending in the spinal cord to excite *(solid lines)* or inhibit *(dashed lines)* the anterior motor neurons that control the body's axial musculature.

Yet some signals from higher areas of the brain can "disinhibit" the medullary system when the brain wishes to excite the pontine system to cause standing. At other times, excitation of the medullary reticular system can inhibit antigravity muscles in certain portions of the body to allow those portions to perform special motor activities. The excitatory and inhibitory reticular nuclei constitute a controllable system that is manipulated by motor signals from the cerebral cortex and elsewhere to provide necessary background muscle contractions for standing against gravity and to inhibit appropriate groups of muscles as needed so that other functions can be performed.

Role of the Vestibular Nuclei to Excite the Antigravity Muscles

All the *vestibular nuclei*, shown in Figure 55–7, function in association with the pontine reticular nuclei to control the antigravity muscles. The vestibular nuclei transmit strong excitatory signals to the antigravity muscles by way of the *lateral* and *medial vestibulospinal tracts* in the anterior columns of the spinal cord, as shown in Figure 55–8. Without this support of the vestibular nuclei, the pontine reticular system would lose much of its excitation of the axial antigravity muscles.

The specific role of the vestibular nuclei, however, is to *selectively* control the excitatory signals to the different antigravity muscles to maintain equilibrium *in response to signals from the vestibular apparatus.* We discuss this more fully later in the chapter.

The Decerebrate Animal Develops Spastic Rigidity

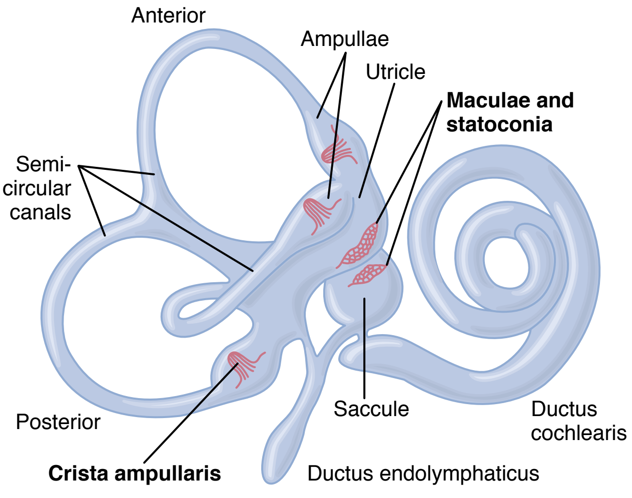
When the brain stem of an animal is sectioned below the midlevel of the mesencephalon, but the pontine and medullary reticular systems as well as the vestibular system are left intact, the animal develops a condition called *decerebrate rigidity.* This rigidity does not occur in all muscles of the body but does occur in the antigravity muscles—the muscles of the neck and trunk and the extensors of the legs.

The cause of decerebrate rigidity is blockage of normally strong input to the medullary reticular nuclei from the cerebral cortex, the red nuclei, and the basal ganglia. Lacking this input, the medullary reticular inhibitor system becomes nonfunctional; full overactivity of the pontine excitatory system occurs, and rigidity develops. We shall see later that other causes of rigidity occur in other neuromotor diseases, especially lesions of the basal ganglia.

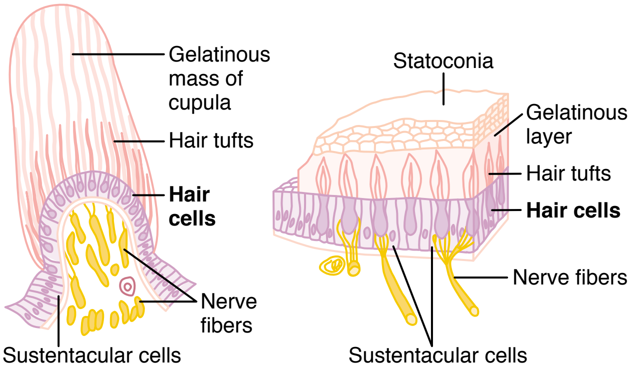
Vestibular Sensations and Maintenance of Equilibrium

Vestibular Apparatus

The vestibular apparatus, shown in Figure 55–9, is the sensory organ for detecting sensations of equilibrium. It is encased in a system of bony tubes and chambers



MEMBRANOUS LABYRINTH



CRISTA AMPULLARIS AND MACULA

Figure 55–9

Membranous labyrinth, and organization of the crista ampullaris and the macula.

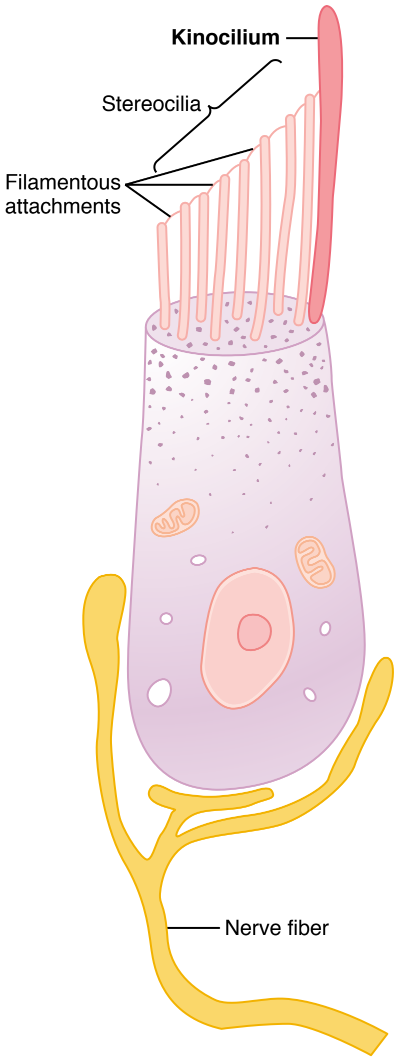


Figure 55–10

Hair cell of the equilibrium apparatus and its synapses with the vestibular nerve.

located in the petrous portion of the temporal bone, called the *bony labyrinth.* Within this system are membranous tubes and chambers called the *membranous labyrinth.* The membranous labyrinth is the functional part of the vestibular apparatus.

The top of Figure 55–9 shows the membranous labyrinth. It is composed mainly of the *cochlea* (ductus cochlearis); three *semicircular canals;* and two large chambers, the *utricle* and *saccule.* The cochlea is the major sensory organ for hearing (see Chapter 52) and has little to do with equilibrium. However, the *semicircular canals,* the *utricle,* and the *saccule* are all integral parts of the equilibrium mechanism.

"Maculae"—Sensory Organs of the Utricle and Saccule for Detecting Orientation of the Head with Respect to Gravity. Located on the inside surface of each utricle and saccule, shown in the top diagram of Figure 55–9, is a small sensory area slightly over 2 millimeters in diameter called a *macula.* The *macula of the utricle* lies mainly in the *horizontal plane* on the inferior surface of the utricle and plays an important role in determining orientation of the head when the head is upright. Conversely, the *macula of the saccule* is located mainly in a *vertical plane* and signals head orientation when the person is lying down.

Each macula is covered by a gelatinous layer in which many small calcium carbonate crystals called *statoconia* are embedded. Also in the macula are thousands of *hair cells,* one of which is shown in Figure 55–10; these project *cilia* up into the gelatinous layer. The bases and sides of the hair cells synapse with sensory endings of the *vestibular nerve.*

The calcified statoconia have a *specific gravity* two to three times the specific gravity of the surrounding fluid and tissues. The weight of the statoconia bends the cilia in the direction of gravitational pull.

Directional Sensitivity of the Hair Cells—Kinocilium. Each hair cell has 50 to 70 small cilia called *stereocilia,* plus one large cilium, the *kinocilium,* as shown in Figure 55–10. The kinocilium is always located to one side, and the stereocilia become progressively shorter toward the other side of the cell. Minute filamentous attachments, almost invisible even to the electron microscope, connect the tip of each stereocilium to the next longer stereocilium and, finally, to the kinocilium. Because of these attachments, when the stereocilia and kinocilium bend in the direction of the kinocilium, the filamentous attachments tug in sequence on the stereocilia, pulling them outward from the cell body. This opens several hundred fluid channels in the neuronal cell membrane around the bases of the stereocilia, and these channels are capable of conducting large numbers of positive ions. Therefore, positive ions pour into the cell from the surrounding endolymphatic fluid, causing *receptor membrane depolarization.* Conversely, bending the pile of stereocilia in the opposite direction (backward to the kinocilium) reduces the tension on the attachments; this closes the ion channels, thus causing *receptor hyperpolarization.*

Under normal resting conditions, the nerve fibers leading from the hair cells transmit continuous nerve impulses at a rate of about 100 per second. When the stereocilia are bent toward the kinocilium, the impulse traffic increases, often to several hundred per second; conversely, bending the cilia away from the kinocilium decreases the impulse traffic, often turning it off completely. Therefore, as the orientation of the head in space changes and the weight of the statoconia bends the cilia, appropriate signals are transmitted to the brain to control equilibrium.

In each macula, each of the hair cells is oriented in a different direction so that some of the hair cells are stimulated when the head bends forward, some are stimulated when it bends backward, others are stimulated when it bends to one side, and so forth. Therefore, a different pattern of excitation occurs in the macular nerve fibers for each orientation of the head in the gravitational field. It is this "pattern" that apprises the brain of the head's orientation in space.

Semicircular Ducts. The three semicircular ducts in each vestibular apparatus, known as the *anterior, posterior,* and *lateral (horizontal) semicircular ducts,* are arranged at right angles to one another so that they represent all three planes in space. When the head is bent forward about 30 degrees, the lateral semicircular ducts are approximately horizontal with respect to the surface of the earth; the anterior ducts are in vertical planes that project *forward and 45 degrees outward,* whereas the posterior ducts are in vertical planes that project *backward and 45 degrees outward.*

Each semicircular duct has an enlargement at one of its ends called the *ampulla,* and the ducts and ampulla are filled with a fluid called *endolymph.* Flow of this fluid through one of the ducts and through its ampulla excites the sensory organ of the ampulla in the following manner: Figure 55–11 shows in each ampulla a small crest called a *crista ampullaris.* On top of this crista is a loose gelatinous tissue mass, the *cupula.* When a person's head begins to rotate in any direction, the inertia of the fluid in one or more of the semicircular ducts causes the fluid to remain stationary while the semicircular duct rotates with the head. This causes fluid to flow from the duct and through the ampulla, bending the cupula to one side, as demonstrated by the position of the colored cupula in Figure 55–11. Rotation of the head in the opposite direction causes the cupula to bend to the opposite side.

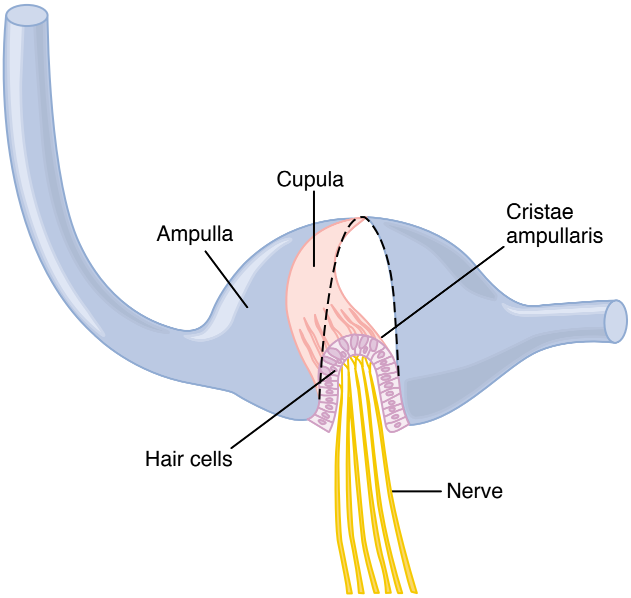


Figure 55–11

Movement of the cupula and its embedded hairs at the onset of rotation.

Into the cupula are projected hundreds of cilia from hair cells located on the ampullary crest. The kinocilia of these hair cells are all oriented in the same direction in the cupula, and bending the cupula in that direction causes depolarization of the hair cells, whereas bending it in the opposite direction hyperpolarizes the cells. Then, from the hair cells, appropriate signals are sent by way of the *vestibular nerve* to apprise the central nervous system of a *change in rotation* of the head and the *rate of change* in each of the three planes of space.

Function of the Utricle and Saccule in the Maintenance of Static Equilibrium

It is especially important that the hair cells are all oriented in different directions in the maculae of the utricles and saccules, so that with different positions of the head, different hair cells become stimulated. The "patterns" of stimulation of the different hair cells apprise the brain of the position of the head with respect to the pull of gravity. In turn, the vestibular, cerebellar, and reticular motor nerve systems of the brain excite appropriate postural muscles to maintain proper equilibrium.

This utricle and saccule system functions extremely effectively for maintaining equilibrium when the head is in the near-vertical position. Indeed, a person can determine as little as half a degree of dysequilibrium when the body leans from the precise upright position.

Detection of Linear Acceleration by the Utricle and Saccule Maculae. When the body is suddenly thrust forward—that is, when the body accelerates—the statoconia, which have greater mass inertia than the surrounding fluid, fall backward on the hair cell cilia, and information of dysequilibrium is sent into the nervous centers, causing the person to feel as though he or she were falling backward. This automatically causes the person to lean forward until the resulting anterior shift of the statoconia exactly equals the tendency for the statoconia to fall backward because of the acceleration. At this point, the nervous system senses a state of proper equilibrium and leans the body forward no farther. Thus, the maculae operate to maintain equilibrium during linear acceleration in exactly the same manner as they operate during static equilibrium.

The maculae *do not* operate for the detection of linear *velocity.* When runners first begin to run, they must lean far forward to keep from falling backward because of initial *acceleration,* but once they have achieved running speed, if they were running in a vacuum, they would not have to lean forward. When running in air, they lean forward to maintain equilibrium only because of air resistance against their bodies; in this instance, it is not the maculae that make them lean but air pressure acting on pressure end-organs in the skin, which initiate appropriate equilibrium adjustments to prevent falling.

Detection of Head Rotation by the Semicircular Ducts

When the head suddenly begins to rotate in any direction (called *angular acceleration*), the endolymph in the semicircular ducts, because of its inertia, tends to remain stationary while the semicircular ducts turn. This causes relative fluid flow in the ducts in the direction opposite to head rotation.

Figure 55–12 shows a typical discharge signal from a single hair cell in the crista ampullaris when an animal is rotated for 40 seconds, demonstrating that (1) even when the cupula is in its resting position, the hair cell emits a tonic discharge of about 100 impulses per second; (2) when the animal begins to rotate, the hairs bend to one side and the rate of discharge increases greatly; and (3) with continued rotation, the excess discharge of the hair cell gradually subsides back to the resting level during the next few seconds.

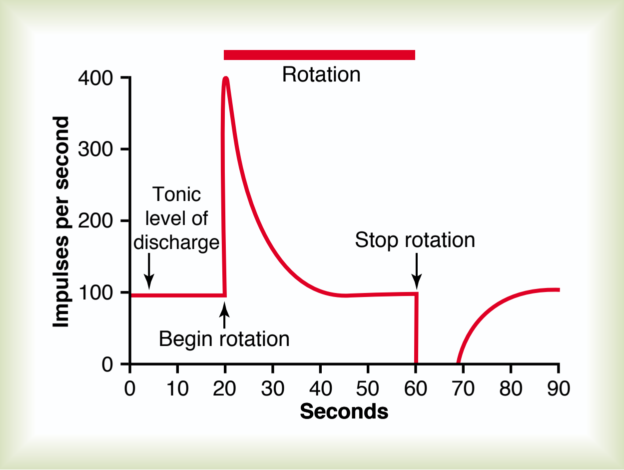


Figure 55–12

Response of a hair cell when a semicircular canal is stimulated first by the onset of head rotation and then by stopping rotation.

The reason for this adaptation of the receptor is that within the first few seconds of rotation, back resistance to the flow of fluid in the semicircular duct and past the bent cupula causes the endolymph to begin rotating as rapidly as the semicircular canal itself; then, in another 5 to 20 seconds, the cupula slowly returns to its resting position in the middle of the ampulla because of its own elastic recoil.

When the rotation suddenly stops, exactly opposite effects take place: The endolymph continues to rotate while the semicircular duct stops. This time, the cupula bends in the opposite direction, causing the hair cell to stop discharging entirely. After another few seconds, the endolymph stops moving and the cupula gradually returns to its resting position, thus allowing hair cell discharge to return to its normal tonic level, as shown to the right in Figure 55–12. Thus, the semicircular duct transmits a signal of one polarity when the head *begins* to rotate and of opposite polarity when it *stops* rotating.

"Predictive" Function of the Semicircular Duct System in the Maintenance of Equilibrium. Because the semicircular ducts do not detect that the body is off balance in the forward direction, in the side direction, or in the backward direction, one might ask: What is the semicircular ducts' function in the maintenance of equilibrium? All they detect is that the person's head is *beginning* or *stopping* to rotate in one direction or another. Therefore, the function of the semicircular ducts is not to maintain static equilibrium or to maintain equilibrium during steady directional or rotational movements. Yet loss of function of the semicircular ducts does cause a person to have poor equilibrium when attempting to perform *rapid, intricate changing* body movements.

We can explain the function of the semicircular ducts best by the following illustration: If a person is running forward rapidly and then suddenly begins to turn to one side, *he or she will fall off balance a fraction of a second later* unless appropriate corrections are made *ahead of time.* But the maculae of the utricle and saccule cannot detect that he or she is off balance until *after* this has occurred. The semicircular ducts, however, will have already detected that the person is turning, and this information can easily apprise the central nervous system of the fact that the person *will* fall off balance within the next fraction of a second or so unless some *anticipatory correction* is made.

In other words, the semicircular duct mechanism *predicts* that dysequilibrium is going to occur and thereby causes the equilibrium centers to make appropriate anticipatory preventive adjustments. In this way, the person need not fall off balance at all before he or she begins to correct the situation.

Removal of the flocculonodular lobes of the cerebellum prevents normal detection of semicircular duct signals but has less effect on detecting macular signals. It is especially interesting that the cerebellum serves as a "predictive" organ for most rapid movements of the body, as well as for those having to do with equilibrium. These other functions of the cerebellum are discussed in the following chapter.

Vestibular Mechanisms for Stabilizing the Eyes

When a person changes his or her direction of movement rapidly or even leans the head sideways, forward, or backward, it would be impossible to maintain a stable image on the retinas unless the person had some automatic control mechanism to stabilize the direction of the eyes' gaze. In addition, the eyes would be of little use in detecting an image unless they remained "fixed" on each object long enough to gain a clear image. Fortunately, each time the head is suddenly rotated, signals from the semicircular ducts cause the eyes to rotate in a direction equal and opposite to the rotation of the head. This results from reflexes transmitted through the *vestibular nuclei* and the *medial longitudinal fasciculus* to the *oculomotor nuclei.* These reflexes are described in Chapter 51.

Other Factors Concerned with Equilibrium

Neck Proprioceptors. The vestibular apparatus detects the orientation and movement *only of the head.* Therefore, it is essential that the nervous centers also receive appropriate information about the orientation of the head with respect to the body. This information is transmitted from the proprioceptors of the neck and body directly to the vestibular and reticular nuclei in the brain stem and indirectly by way of the cerebellum.

Among the most important proprioceptive information needed for the maintenance of equilibrium is that transmitted by *joint receptors of the neck.* When the head is leaned in one direction by bending the neck, impulses from the neck proprioceptors keep the signals originating in the vestibular apparatus from giving the person a sense of dysequilibrium. They do this by transmitting signals that exactly oppose the signals transmitted from the vestibular apparatus. However, *when the entire body* leans in one direction, the impulses from the vestibular apparatus *are not opposed* by signals from the neck proprioceptors; therefore, in this case, the person does perceive a change in equilibrium status of the entire body.

Proprioceptive and Exteroceptive Information from Other Parts of the Body. Proprioceptive information from parts of the body other than the neck is also important in the maintenance of equilibrium. For instance, pressure sensations from the footpads tell one (1) whether weight is distributed equally between the two feet and (2) whether weight on the feet is more forward or backward.

Exteroceptive information is especially necessary for the maintenance of equilibrium when a person is running. The air pressure against the front of the body signals that a force is opposing the body in a direction different from that caused by gravitational pull; as a result, the person leans forward to oppose this.

Importance of Visual Information in the Maintenance of Equilibrium. After destruction of the vestibular apparatus, and even after loss of most proprioceptive information from the body, a person can still use the visual mechanisms reasonably effectively for maintaining equilibrium. Even a slight linear or rotational movement of the body instantaneously shifts the visual images on the retina, and this information is relayed to the equilibrium centers. Some people with bilateral destruction of the vestibular apparatus have almost normal equilibrium as long as their eyes are open and all motions are performed slowly. But when moving rapidly or when the eyes are closed, equilibrium is immediately lost.

Neuronal Connections of the Vestibular Apparatus with the Central Nervous System

Figure 55–13 shows the connections in the hindbrain of the vestibular nerve. Most of the vestibular nerve fibers terminate in the brain stem in the *vestibular nuclei*, which are located approximately at the junction of the medulla and the pons. Some fibers pass directly to the brain stem reticular nuclei without synapsing and also to the cerebellar fastigial, uvular, and flocculonodular lobe nuclei. The fibers that end in the brain stem vestibular nuclei synapse with second-order neurons that also send fibers into the cerebellum, the vestibulospinal tracts, the medial longitudinal fasciculus, and

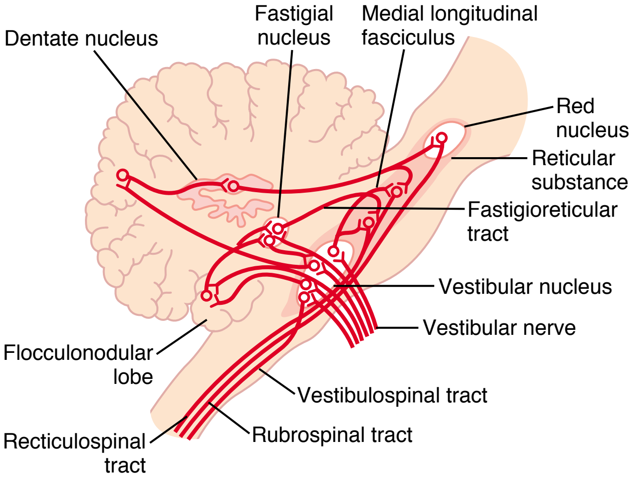


Figure 55–13

Connections of vestibular nerves through the vestibular nuclei (the large oval white area) with other areas of the central nervous system.

other areas of the brain stem, particularly the reticular nuclei.

The primary pathway for the equilibrium reflexes begins in the vestibular nerves, where the nerves are excited by the vestibular apparatus. The pathway then passes to the vestibular nuclei and cerebellum. Next, signals are sent into the reticular nuclei of the brain stem, as well as down the spinal cord by way of the vestibulospinal and reticulospinal tracts. The signals to the cord control the interplay between facilitation and inhibition of the many antigravity muscles, thus automatically controlling equilibrium.

The *flocculonodular* lobes of the cerebellum are especially concerned with dynamic equilibrium signals from the semicircular ducts. In fact, destruction of these lobes results in almost exactly the same clinical symptoms as destruction of the semicircular ducts themselves. That is, severe injury to either the lobes or the ducts causes loss of dynamic equilibrium during *rapid changes in direction of motion* but does not seriously disturb equilibrium under static conditions. It is believed that the *uvula* of the cerebellum plays a similar important role in static equilibrium.

Signals transmitted upward in the brain stem from both the vestibular nuclei and the cerebellum by way of the *medial longitudinal fasciculus* cause corrective movements of the eyes every time the head rotates, so that the eyes remain fixed on a specific visual object. Signals also pass upward (either through this same tract or through reticular tracts) to the cerebral cortex, terminating in a primary cortical center for equilibrium located in the parietal lobe deep in the sylvian fissure on the opposite side of the fissure from the auditory area of the superior temporal gyrus. These signals apprise the psyche of the equilibrium status of the body.

Functions of Brain Stem Nuclei in Controlling Subconscious, Stereotyped Movements

Rarely, a baby is born without brain structures above the mesencephalic region, a condition called *anencephaly.* Some of these babies have been kept alive for many months. They are able to perform some stereotyped movements for feeding, such as suckling, extrusion of unpleasant food from the mouth, and moving the hands to the mouth to suck the fingers. In addition, they can yawn and stretch. They can cry and can follow objects with movements of the eyes and head. Also, placing pressure on the upper anterior parts of their legs causes them to pull to the sitting position. It is clear that many of the stereotyped motor functions of the human being are integrated in the brain stem.

References

Alitto HJ, Usrey WM: Corticothalamic feedback and sensory processing. Curr Opin Neurobiol 13:440, 2003.

Angelaki DE, Dickman JD: Gravity or translation: central processing of vestibular signals to detect motion or tilt. J Vestib Res 13:245, 2003.

Barmack NH: Central vestibular system: vestibular nuclei and posterior cerebellum. Brain Res Bull 60:511, 2003.

Blake DT, Byl NN, Merzenich MM: Representation of the hand in the cerebral cortex. Behav Brain Res 135:179, 2002.

Boyle R: Vestibulospinal control of reflex and voluntary head movement. Ann N Y Acad Sci 942:364, 2001.

Cullen KE, Roy JE: Signal processing in the vestibular system during active versus passive head movements. J Neurophysiol 91:1919, 2004.

Garwicz M: Spinal reflexes provide motor error signals to cerebellar modules—relevance for motor coordination. Brain Res Brain Res Rev 40:152, 2002.

Johansen-Berg H: Motor physiology: a brain of two halves. Curr Biol 13:R802, 2003.

Raineteau O, Schwab ME: Plasticity of motor systems after incomplete spinal cord injury. Nat Rev Neurosci 2:263, 2001.

Raphael Y, Altschuler RA: Structure and innervation of the cochlea. Brain Res Bull 60:397, 2003.

Robles L, Ruggero MA: Mechanics of the mammalian cochlea. Physiol Rev 81:1305, 2001.

Salenius S, Hari R: Synchronous cortical oscillatory activity during motor action. Curr Opin Neurobiol 13:678, 2003.

Sanes JN: Neocortical mechanisms in motor learning. Curr Opin Neurobiol 13:225, 2003.

Schieber MH: Motor control: basic units of cortical output? Curr Biol 14:R353, 2004.

Scott SH: The role of primary motor cortex in goal-directed movements: insights from neurophysiological studies on non-human primates. Curr Opin Neurobiol 13:671, 2003.

Umilta MA: Frontal cortex: goal-relatedness and the cortical motor system. Curr Biol 14:R204, 2004.

Yates BJ, Miller AD, Lucot JB: Physiological basis and pharmacology of motion sickness: an update. Brain Res Bull 47:395, 1998.