

Principles of Applied Vestibular Physiology

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Key Points

- The vestibular system primarily drives reflexes to maintain stable vision and posture.
- By modulating the nonzero baseline firing of vestibular afferent nerve fibers, semicircular canals encode rotation of the head, and otolith organs encode linear acceleration and tilt.
- Stimulation of a semicircular canal produces eye movements in the plane of that canal.
- A semicircular canal normally is excited by head rotation about the axis of that canal bringing the forehead toward the ipsilateral side.
- Any stimulus that excites a semicircular canal's afferents will be interpreted as excitatory rotation in the plane of that canal.
- High-acceleration head rotation in the excitatory direction of a canal elicits a greater response than does the same rotation in the inhibitory direction.
- The response to simultaneous canal stimuli is approximately the sum of the responses to each stimulus alone.
- Nystagmus as a result of dysfunction of the semicircular canals has a fixed axis and direction with respect to the head.
- Brainstem circuitry boosts low-frequency vestibuloocular reflex performance through velocity storage and neural integration. Failure of these mechanisms suggests a central pathologic process.
- The utricle senses both head tilt and translation, but loss of unilateral utricular function is interpreted by the brain as a head tilt toward the opposite side.
- Sudden changes in saccular activity evoke changes in postural tone.
- The normal vestibular system can rapidly adjust the vestibular reflexes according to the context, but adaptation to unilateral loss of vestibular function may be slow and is susceptible to decompensation.

PRINCIPLE 1: THE VESTIBULAR SYSTEM PRIMARILY DRIVES REFLEXES TO MAINTAIN STABLE VISION AND POSTURE

- ▶ *vestibuloocular reflex* (VOR), which stabilizes gaze (eye position in space).
- ▶ the *vestibulocolic reflex* or to lower spinal motor neurons
- ▶ to generate the *vestibulospinal reflexes*. These reflexes stabilize posture and facilitate gait
- ▶ Proprioceptors in the neck mediate a *cervicoocular reflex* that can augment the deficient VOR
- ▶ Postural information may be supplied by gravity receptors in the major blood vessels and abdominal viscera

- ▶ *smooth pursuit* is a type of reflexive eye movement that helps to stabilize images on the retina
- ▶ The stimulus for this reflex is the difference between the velocity of the visual target and the velocity of the eye, which is called *retinal slip velocity*.
- ▶ Smooth visual pursuit functions best for low-frequency and slow head movements.
- ▶ the vestibular system is essential for gaze stabilization during *high-frequency, high-velocity, and high acceleration* head movements.

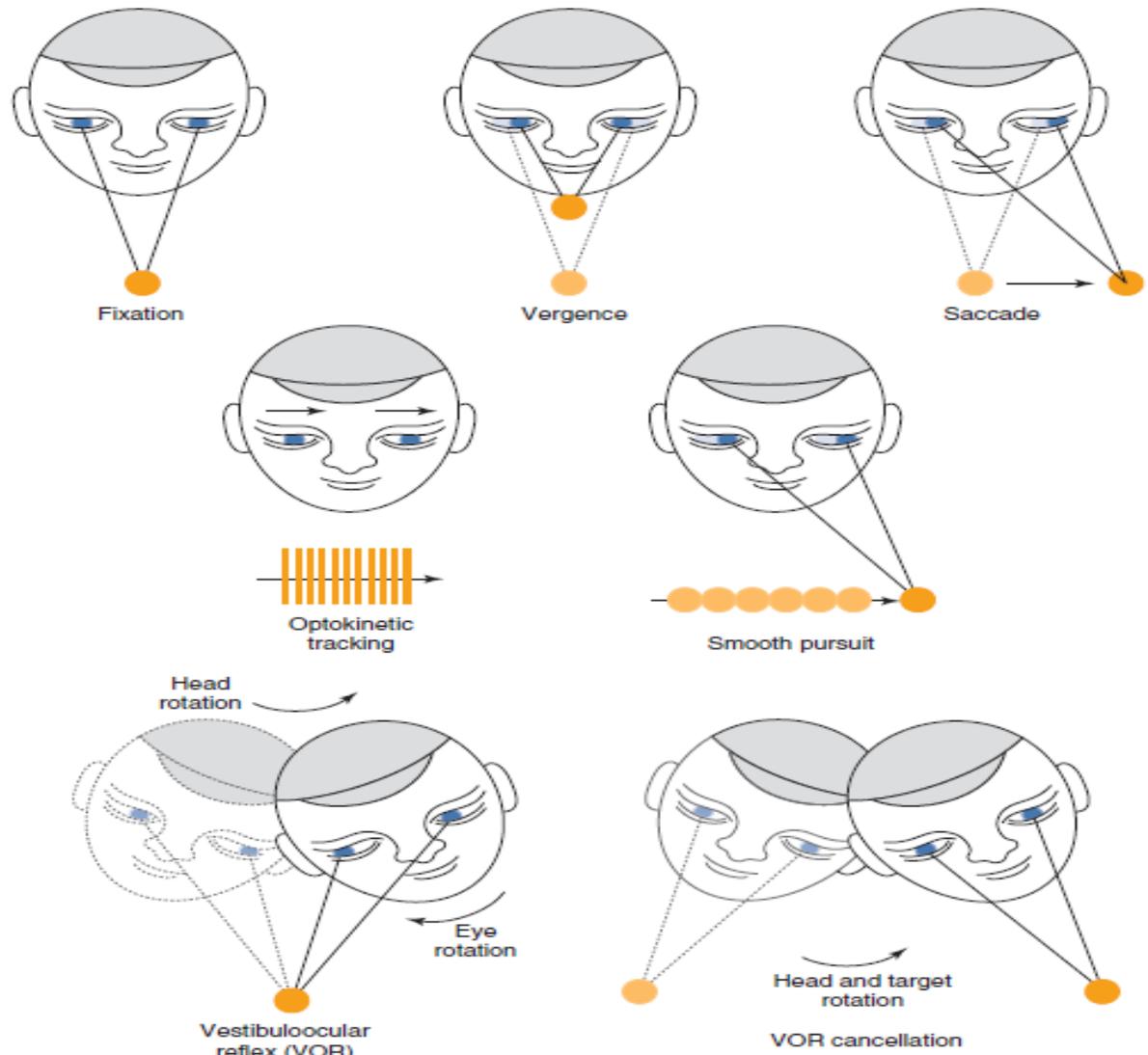


FIGURE 164-1. Schematic depiction of the functional classes of eye movements. Basic research in the neurophysiology of oculomotor control and clinical studies of eye movement disorders have been enhanced by the recognition of functionally distinct subsystems. Seven types of eye movements are shown.

Encoding of linear acceleration
due to tilt and translation

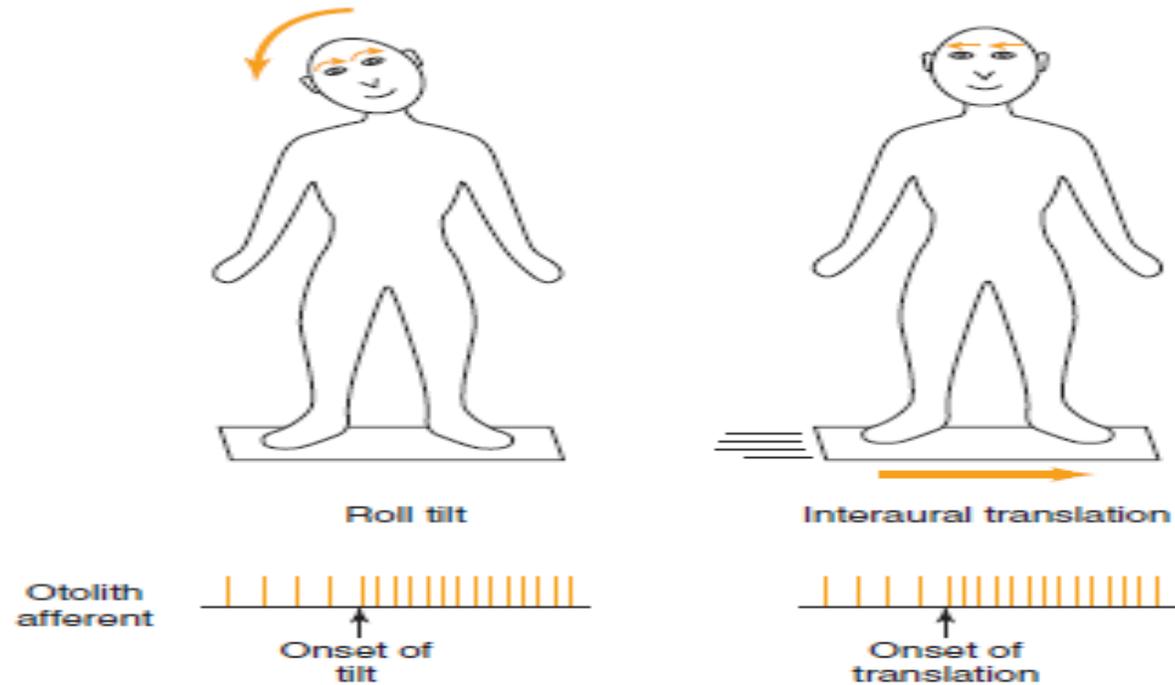
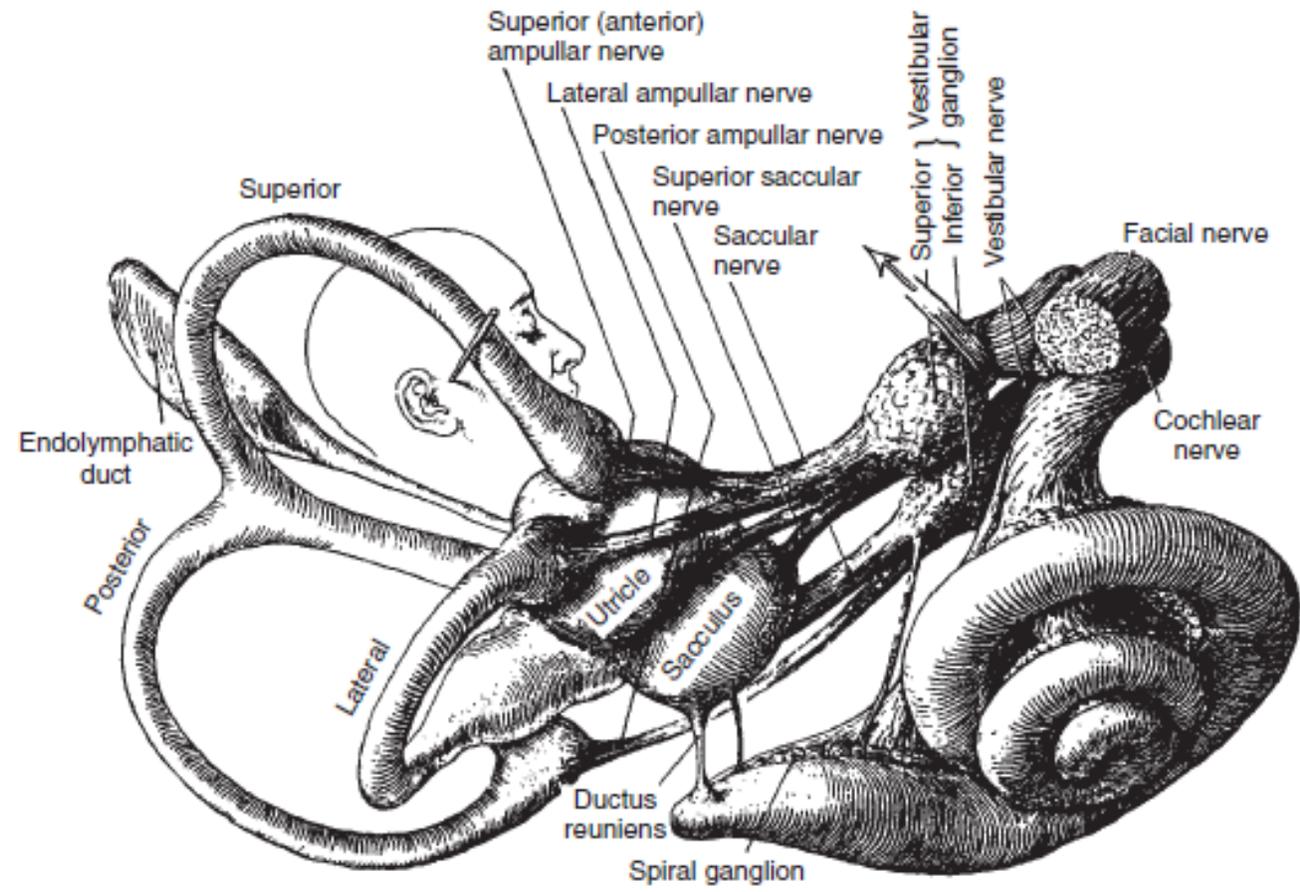


FIGURE 164-3. Otolith afferents respond to linear acceleration. Identical changes in otolith afferent activity can result from head movements that change the orientation of the head relative to gravity (roll tilt) and from linear translational movement (interaural translation). The compensatory eye movements evoked by these two types of head movements are quite different. (From Minor LB: Physiological principles of vestibular function on earth and in space. *Otolaryngol Head Neck Surg* 1998;118:54.)



PRINCIPLE 2: BY MODULATING THE NONZERO BASELINE FIRING OF VESTIBULAR AFFERENT NERVE FIBERS, SEMICIRCULAR CANALS ENCODE ROTATION OF THE HEAD AND OTOLITH ORGANS ENCODE LINEAR ACCELERATION AND TILT

- ▶ Semicircular canals primarily sense **rotational acceleration** of the head. The utricle and saccule primarily sense **linear acceleration** in horizontal and **vertical (superoinferior)** directions
- ▶ head accelerates in the plane of a semicircular canal, inertia causes the endolymph in the canal to lag behind the motion of the membranous canal, much as coffee in a mug initially remains in place as the mug is rotated about.
- ▶ Stereocilia within a bundle are linked to one another by protein strands called *tip links* that span from the side of a taller stereocilium to the tip of its shorter neighbor in the array.

- ▶ deflected in the open or “on” direction, which is toward the tallest stereocilium, cations—which include potassium ions from the potassium-rich endolymph—rush in through the gates, and the membrane potential of the hair cell becomes more positive

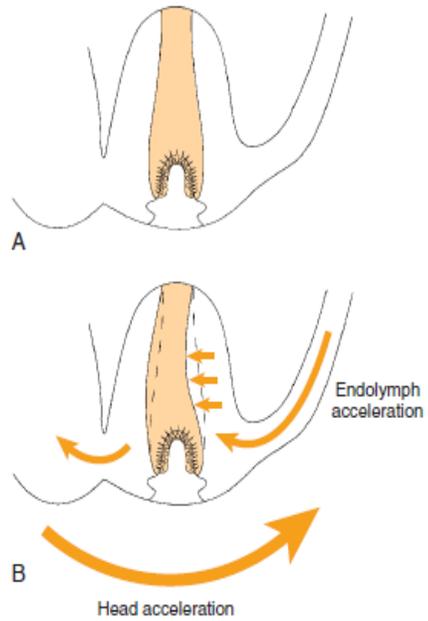


FIGURE 163-2. **A**, The cupula spans the lumen of the ampulla from the crista to the membranous labyrinth. **B**, Head acceleration exceeds endolymph acceleration. The relative flow of endolymph in the canal is therefore opposite to the direction of head acceleration. This flow produces a pressure across the elastic cupula, which deflects in response.

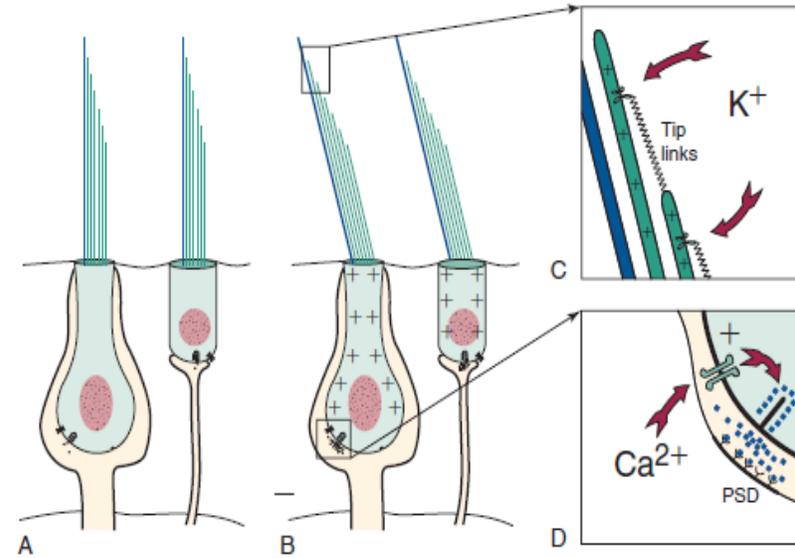


FIGURE 163-3. Sensory transduction by vestibular hair cells. **A**, Some baseline release of excitatory glutamate from the hair cell synapses onto the vestibular afferents at rest. **B**, Hair cells are depolarized when the stereocilia are deflected in the "on" direction, toward the kinocilium (green). **C**, This occurs because the stretched tip links mechanically open cationic channels in the stereocilia membranes. The influx of potassium ions raises the hair cell's membrane potential. **D**, The increased membrane potential activates voltage-sensitive calcium channels in the basolateral membrane of the cell. Synaptic release of glutamate increases, and receptors in the postsynaptic density (PSD) on the afferent increase its membrane potential, which in turn increases afferent firing rate.

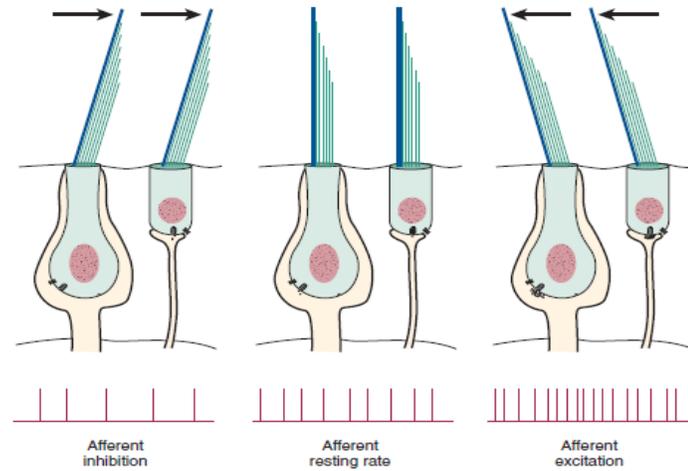


FIGURE 163-8. A vestibular afferent nerve fires actively at rest (center) at a rate modulated by sensory transduction. The afferent is inhibited when the stereocilia of its hair cells are deflected in the "off" direction, away from the kinocilium (left panel) and excited when the stereocilia are deflected in the "on" direction, toward the kinocilium (right panel).

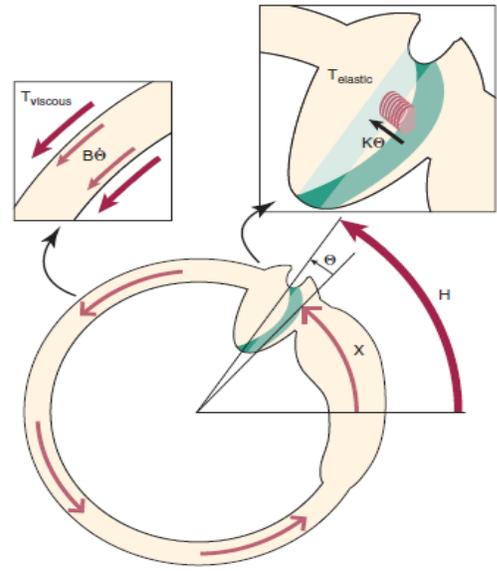


FIGURE 163-9. The torsional pendulum model of the mechanical forces that act on the cupula and endolymph of the left horizontal canal during leftward angular head acceleration as seen from above. As the head rotates through space over an angle H , endolymph inside the canal also rotates through space but over a slightly smaller angle, X . The difference between the angles through which the head and endolymph rotate in space is Θ , which approximates the angular deflection of the cupula. This creates an elastic torque proportional to the deflection: $T_{\text{elastic}} = K\Theta$. A viscous or drag torque is produced by the relative flow of endolymph along the walls of the canal and is proportional to the endolymph velocity relative to the canal: $T_{\text{viscous}} = B\dot{\Theta}$. The sum of these torques will equal the moment of inertia of the cupula and endolymph times their acceleration: $K\Theta + B\dot{\Theta} + I\ddot{X} = I\ddot{H} - I\ddot{\Theta}$.

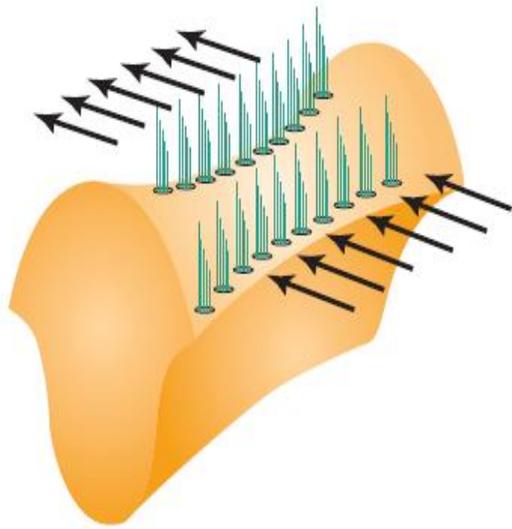


FIGURE 163-4. Morphologic polarization of the stereociliary bundles in the crista ampullaris. The "on" direction of deflection is always toward the kinocilium, which is next to the tallest stereocilium. Hair cells on the crista ampullaris of a given semicircular canal have all their stereocilia polarized in the same direction.

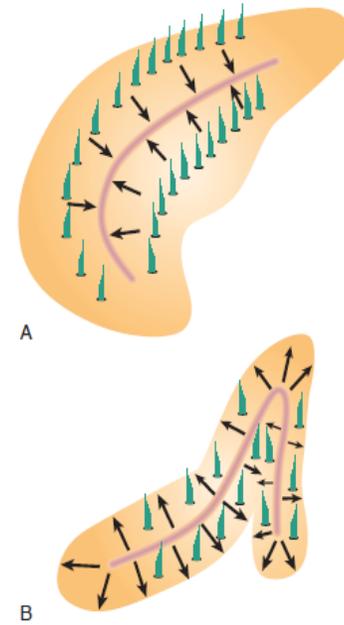


FIGURE 163-6. Morphologic polarizations of the stereociliary bundles in the maculae of the utricle (A) and saccule (B). The "on" direction of stereociliary deflection is indicated by the arrows. In the utricle (A), hair cells are excited by stereociliary deflection toward the striola (*curving central zone*). In the saccule (B), hair cells are excited by stereociliary deflection away from the striola.

PRINCIPLE 3: STIMULATION OF A SEMICIRCULAR CANAL PRODUCES EYE MOVEMENTS IN THE PLANE OF THAT CANAL

- ▶ Ewald's first law.
- ▶ The left anterior canal is roughly coplanar with the right posterior canal in the left anterior-right posterior (LARP) plane
- ▶ When the head is upright, the horizontal canal (or lateral canal [LC]) is tilted approximately 20 degrees upward from the horizontal plane at its anterior end.
- ▶ The vertical canals are oriented in planes roughly 45 degrees from the midsagittal plane. The right anterior canal (AC) and left posterior canal (PC) lie in the same plane, the right anterior-left posterior plane
- ▶ as the *push-pull* arrangement of the canals.

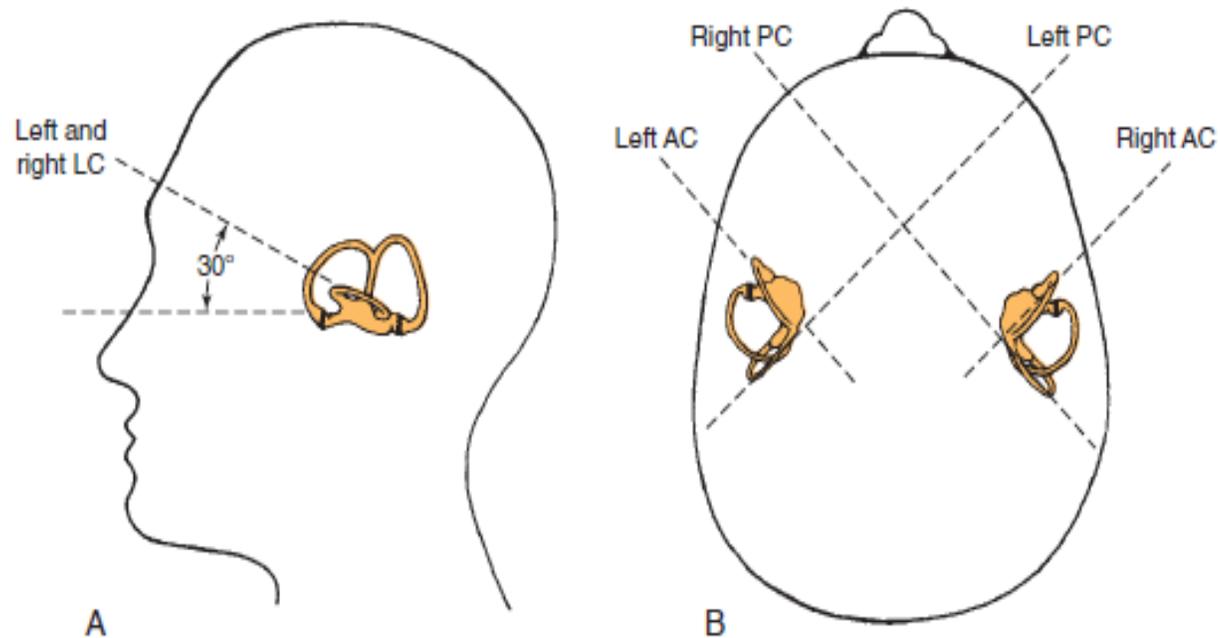


FIGURE 130-2. Orientation of semicircular canals. **A**, The horizontal canal is tilted 30 degrees upward from a horizontal plane at its anterior end. **B**, Vertical canals are oriented at roughly 45 degrees from the midsagittal plane. AC, anterior canal; LC, lateral canal; PC, posterior canal. (Modified from Barber HO, Stockwell CW. *Manual of electronystagmography*. St Louis: Mosby-Year Book; 1976.)

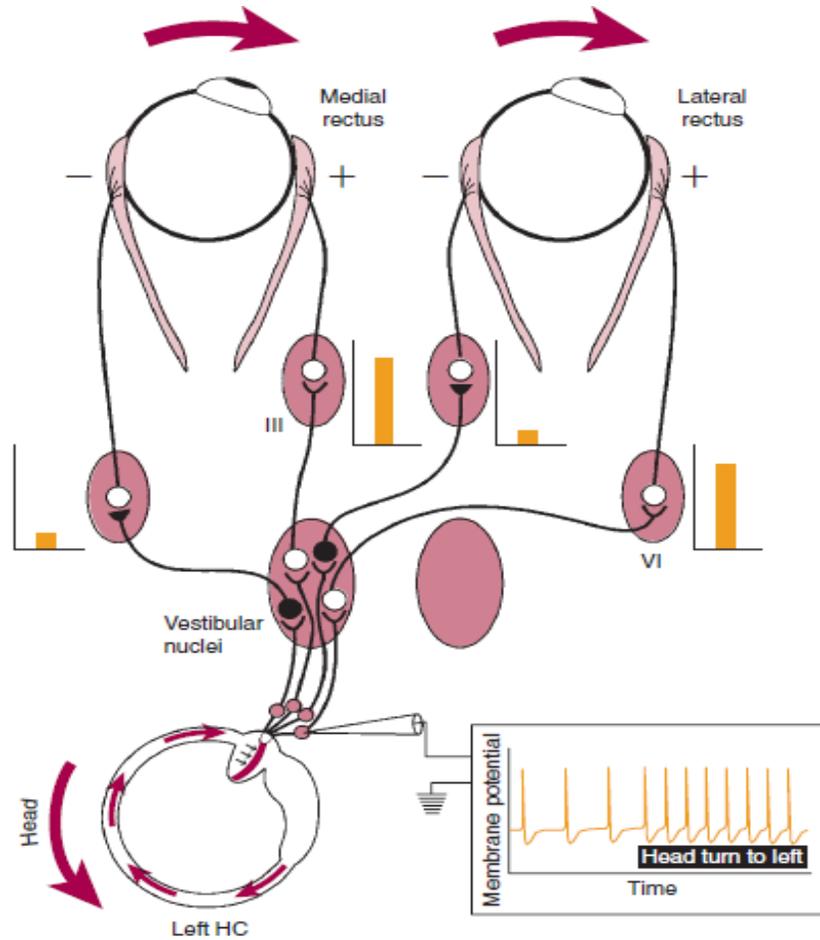


FIGURE 163-15. Neural connections in the direct pathway for the vestibuloocular reflex from excitation of the left horizontal canal (HC). As seen from above, a leftward head rotation produces relative endolymph flow in the left HC that is clockwise and toward the utricle. The cupular deflection excites the hair cells in the left HC ampulla, and the firing rate in the afferents increases (*inset*). Excitatory interneurons in the vestibular nuclei connect to motor neurons for the medial rectus muscle in the ipsilateral third nucleus (III) and lateral rectus muscle in the contralateral sixth nucleus (VI). Firing rates for these motor neurons increase (*small bar graphs*). The respective muscles contract and pull the eyes clockwise, opposite the head, during the slow phases of nystagmus. Inhibitory interneurons in the vestibular nuclei connect to motoneurons for the left lateral rectus and right medial rectus. Their firing rates decrease, and these antagonist muscles relax to facilitate the eye movement.

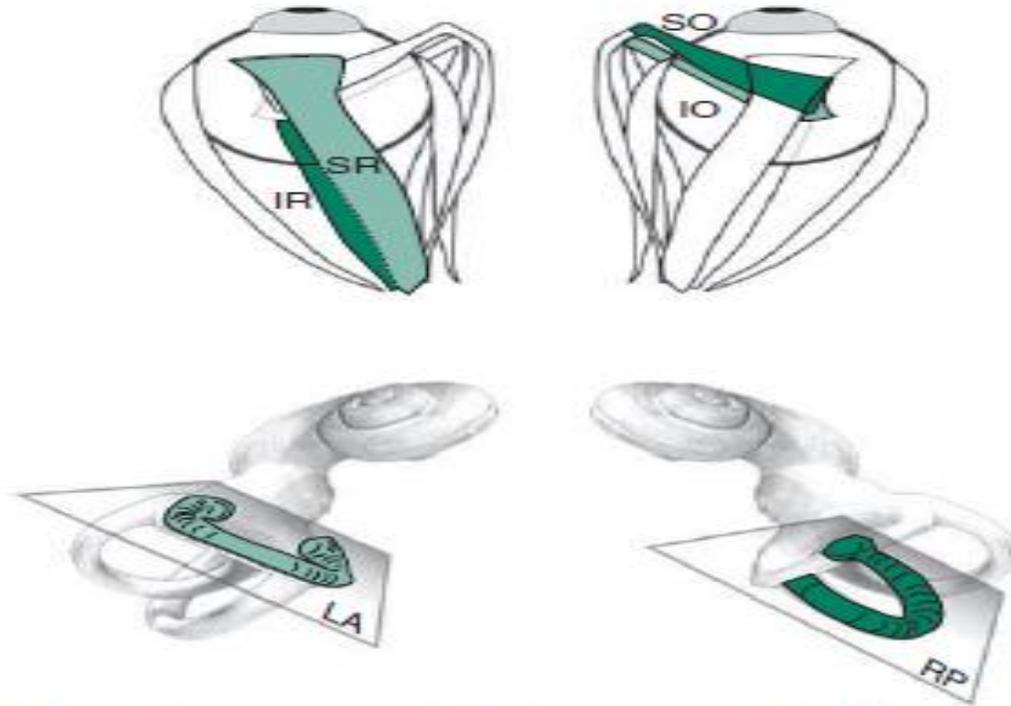


FIGURE 163-17. The left anterior–right posterior canal (LARP) plane aligns with the pulling directions of the left superior rectus (SR) and inferior rectus (IR) muscles and the right superior oblique (SO) and inferior oblique (IO) muscles. As indicated by the shading, excitation of the left anterior canal and inhibition of the right posterior canal causes contraction of the left SR and right IO muscles and relaxation of the darker-shaded antagonists. The result will be an upward movement of the eyes in the LARP plane. Excitation of the right posterior canal will produce the opposite effect.

PRINCIPLE 4: A SEMICIRCULAR CANAL NORMALLY IS EXCITED BY HEAD ROTATION ABOUT THE AXIS OF THAT CANAL BRINGING THE FOREHEAD TOWARD THE IPSILATERAL SIDE

- ▶ In the horizontal canal, the taller ends of the bundles point toward the utricle.
- ▶ Flow of endolymph (relative to the head) toward the **ampullaampullopetal** flow (from Latin *petere*, “to seek”) therefore excites the horizontal canal afferents
- ▶ The vertical canals, however, have the opposite pattern of hair cell polarization
- ▶ The taller ends of the bundles point away from the utricle, so that flow away from the ampulla (**ampullofugal**) excites their afferents
- ▶ the left posterior canal, whose ampulla is at its posterior en

PRINCIPLE 5: ANY STIMULUS THAT EXCITES A SEMICIRCULAR CANAL'S AFFERENTS WILL BE INTERPRETED AS EXCITATORY ROTATION IN THE PLANE OF THAT CANAL

- ▶ rapid resetting movements occur that take the eyes back toward their neutral positions in the orbits.
- ▶ The quick resetting movements, similar to saccades, are *quick phases* of nystagmus, and the vestibular-driven slower movements are *slow phases*.
- ▶ Unfortunately, convention dictates that **nystagmus direction** is described according to the direction of the **quick phases**

- ▶ **Posterior Canal Benign Paroxysmal Positional Vertigo**
- ▶ the left PC, excitatory rotation consists of rolling the head toward the left while bringing the nose up.
- ▶ To keep the eyes stable in space, the VOR generates slow phases that move the **eyes down and roll them clockwise** (with respect to the patient's head).
- ▶ The quick phases are opposite; they beat **upward and counterclockwise** with respect to the patient's head

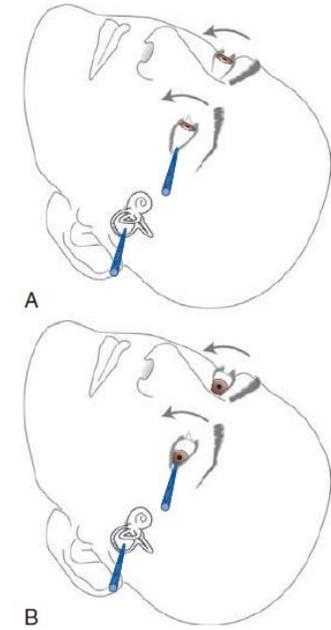
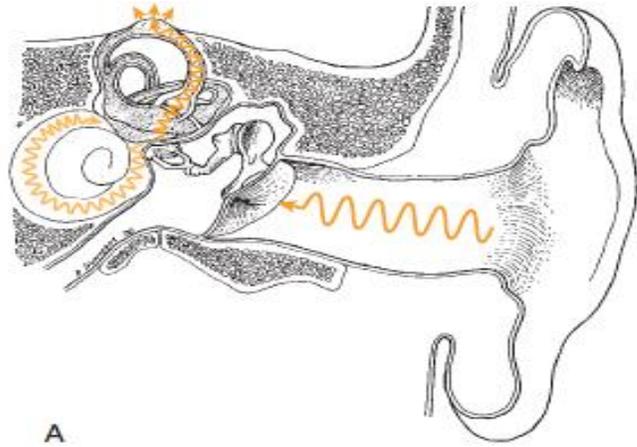
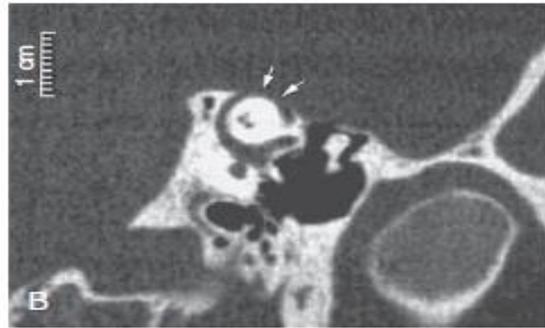


FIGURE 163-18. Excitation of the left posterior canal (PC) by moving canaliths in benign paroxysmal positional vertigo causes slow-phase eye movements downward in the plane of the affected PC. The eyes rotate around an axis parallel to the one going through the center of the affected PC. **A,** When gaze is directed perpendicular to the axis of eye rotation, the pupil appears to move up and down in an eye-fixed reference frame. **B,** When gaze is directed parallel to the axis of eye rotation, the pupil appears to move torsionally in an eye-fixed reference frame. In either case, the eyes rotate around the same axis when considered in a canal-fixed frame of reference.



A



B

FIGURE 163-19. **A,** In superior canal dehiscence syndrome, sound waves can excite the superior canal, because the “third mobile window” created by the dehiscence allows some sound pressure to be dissipated along a route through the superior canal in addition to the conventional route through the cochlea. **B,** Computed tomography scan demonstrates dehiscence (arrows) of the superior canal. (**A,** Courtesy Dr. B. Dunham.)

Nystagmus During Caloric Testing

- ▶ That endolymph becomes lighter (by heating) or heavier (by cooling) than the endolymph in the rest of the labyrinth.
- ▶ endolymph in the lateral part of the canal made lighter by warming rises toward the ampulla.
- ▶ the slow phases of nystagmus, are in the horizontal canal plane and toward the contralateral side.
- ▶ The mnemonic COWS—cold opposite, warm same—can be used to recall the direction of the beating of the nystagmus
- ▶ A major advantage is a truly unilateral stimulus.

PRINCIPLE 6: HIGH ACCELERATION HEAD ROTATION IN THE EXCITATORY DIRECTION OF A CANAL ELICITS A GREATER RESPONSE THAN THE SAME ROTATION IN THE INHIBITORY DIRECTION

- ▶ Ewald's second law, indicates an *excitation-inhibition asymmetry*

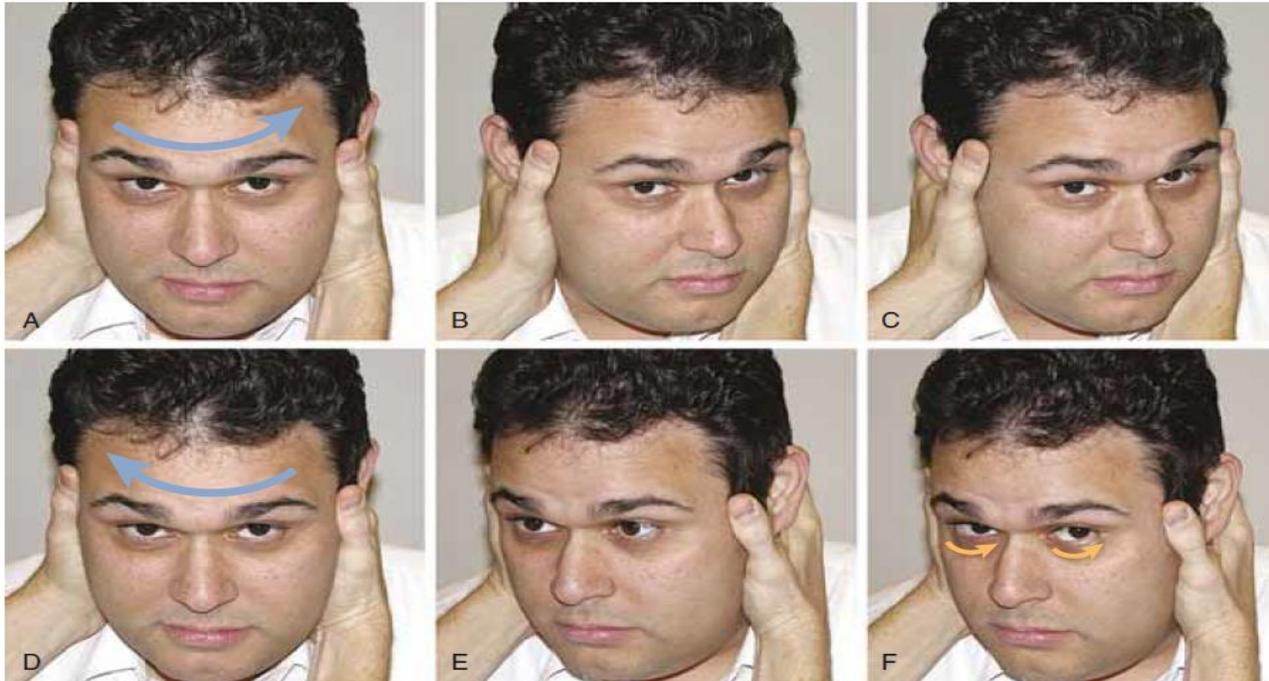


FIGURE 163-22. In the clinical version of the head-thrust test, the examiner asks the subject to fix the gaze on the examiner's nose. The examiner rapidly turns the subject's head but only by approximately 10 to 15 degrees; larger angles of rotation are unnecessary and may risk injury to the neck. The acceleration must be ≥ 3000 degrees/sec², and the peak velocity must be 150 to 300 degrees/sec, meaning that the rotation must be finished in 150 ms. **A through C** show a head thrust to the left, exciting the left horizontal canal (HC). The eyes stay on the examiner's nose throughout the maneuver, indicating normal left HC function. **D through F** show a head thrust to the right, exciting the right HC. The eyes do not stay on target but move with the head during the head thrust (**D** and **E**). A refixation saccade brings the eyes back on target after completion of the head movement (**F**). This is a "positive" head-thrust sign for the right HC, which indicates hypofunction of that canal.

PRINCIPLE 7: THE RESPONSE TO SIMULTANEOUS CANAL STIMULI IS APPROXIMATELY THE SUM OF THE RESPONSES TO EACH STIMULUS ALONE

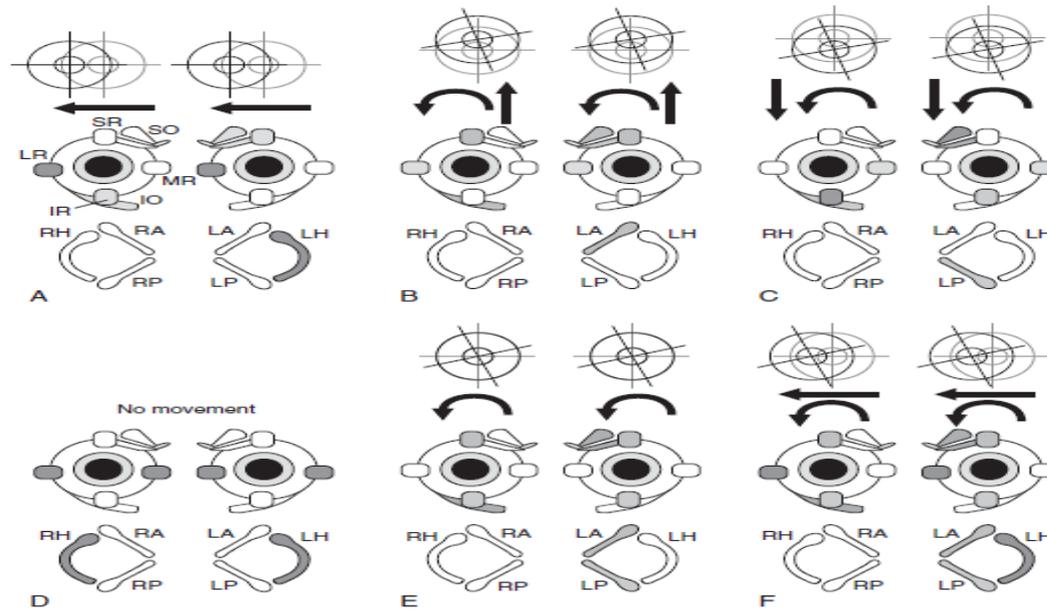


FIGURE 163-25. Nystagmus slow phases observed for excitation of individual semicircular canals. In the bottom row of each panel (A through F), shading indicates the excited canals. In the second row, a diagram of the extraocular muscles depicts which muscles are activated (darker shading indicates stronger activation). In the top row, the resultant yaw, pitch, and/or roll eye movements are indicated. **A**, Excitation of the left horizontal (LH) canal causes rightward slow phases mainly as a result of strong activation of right lateral rectus (LR) muscle and left medial rectus (MR) muscle. **B**, Excitation of the left anterior (LA) canal causes upward/clockwise (from patient's perspective) slow phases because of the combined action of the right inferior oblique (IO) muscle and superior rectus (SR) muscle and the left superior oblique (SO) muscle and SR. **C**, Excitation of the left posterior (LP) canal causes downward/clockwise (from patient's perspective) slow phases as a result of the combined action of the right IO and inferior rectus (IR) muscle and the left SO and IR. **D**, Equal stimulation of left horizontal (LH) and right horizontal (RH) canals elicits antagonistic contraction of MR and LR bilaterally, yielding no nystagmus. **E**, Combined equal excitation of left anterior (LA) and left posterior (LP) canals excites muscle activity that is the sum of each canal's individual effect; upward and downward pulls cancel, which results in a purely clockwise nystagmus. **F**, Combined equal excitation of all three left canals causes a right-clockwise slow phase, the expected result of summing activity for each individual canal. RA, right anterior canal; RP, right posterior canal. (Modified from Cohen B, Suzuki J-I, Bender MB: Eye movements from semicircular canal nerve stimulation in the cat. *Ann Otol Rhinol Laryngol* 1964;73:153; data adjusted to human head frame of reference.)

PRINCIPLE 8: NYSTAGMUS AS A RESULT OF DYSFUNCTION OF SEMICIRCULAR CANALS HAS A FIXED AXIS AND DIRECTION WITH RESPECT TO THE HEAD

- ▶ *direction-fixed* nystagmus
- ▶ This principle helps to distinguish nystagmus from a peripheral vestibular disorder from nystagmus as a result of a central disorder.
- ▶ It is important to note that the *magnitude* of the nystagmus is *not* fixed depending on gaze

PRINCIPLE 9: BRAINSTEM CIRCUITRY BOOSTS LOW-FREQUENCY VESTIBULOOCULAR REFLEX PERFORMANCE THROUGH VELOCITY STORAGE AND NEURAL INTEGRATION; FAILURE OF THESE MECHANISMS SUGGESTS CENTRAL PATHOLOGY

- ▶ indirect pathway” through the brainstem circuits also must account for the poor performance of the vestibular end organs at low frequencies
- ▶ *velocity storage* and *velocity-to-position integration*.
- ▶ Postrotatory nystagmus, **post-head-shaking nystagmus**, and **Alexander’s law**
- ▶ cardinal signs that differentiates peripheral from central causes of nystagmus
- ▶ **Velocity Storage**. For head rotations at frequencies below approximately 0.1 Hz
- ▶ Velocity rotation, the cupula initially deflects but then returns back to its resting position, with a time constant of approximately 13 seconds. Thus nystagmus in response to a constant-velocity rotation would be expected to disappear after approximately 30 seconds

► pontine reticular formation (PPRF)

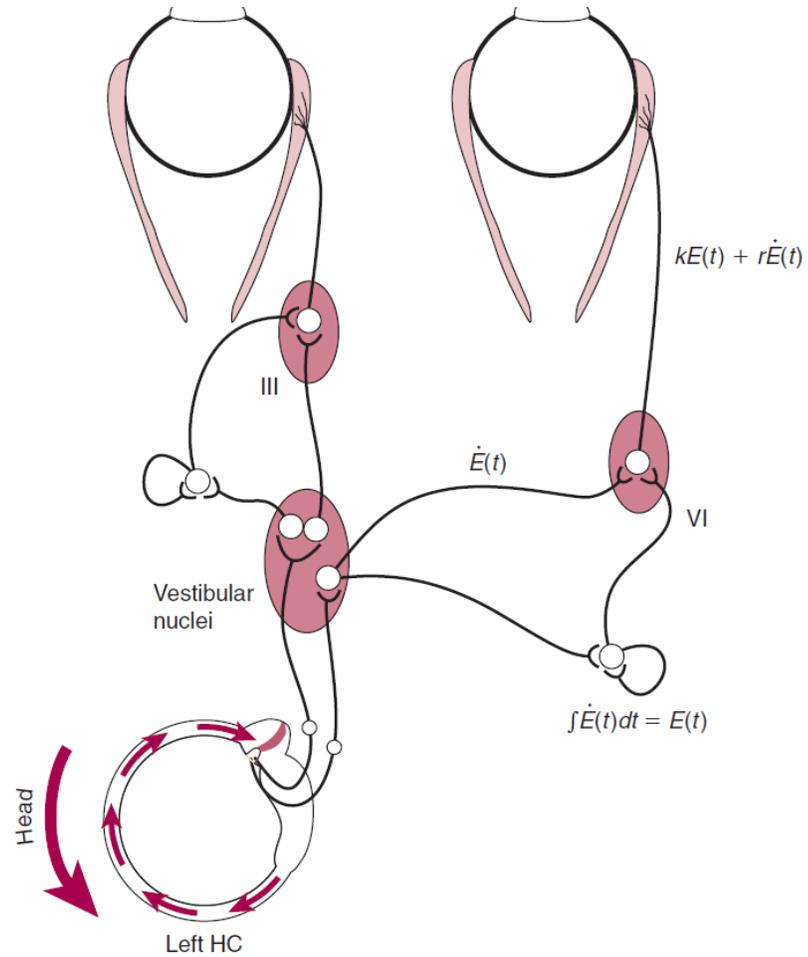


FIGURE 163-27. Signals from the canals also pass through direct and indirect pathways to the ocular motor nuclei. (The direct excitatory pathway for the horizontal vestibuloocular reflex is depicted in detail in [Figure 163-15](#).) The indirect pathway through the velocity-to-position integrator provides the final ocular motor signal with a component proportional to eye position. HC, horizontal canal.

- ▶ **Head-Shake Nystagmus** :rotates the subject's head horizontally at 1 to 2 Hz for 10 to 20 cycles of rotation
- ▶ As a result, when the head stops rotating, the nystagmus is as would be expected for continued rotation toward the intact side:
- ▶ caloric testing measures the function of an isolated semicircular canal at relatively low frequency
- ▶ the HTT uses rapid, brief rotations with frequency content in the range of 3 to 5 Hz.
- ▶ By providing information about the function of the labyrinth at 1 to 2 Hz, the head-shaking test may provide information not available from the other two tests.

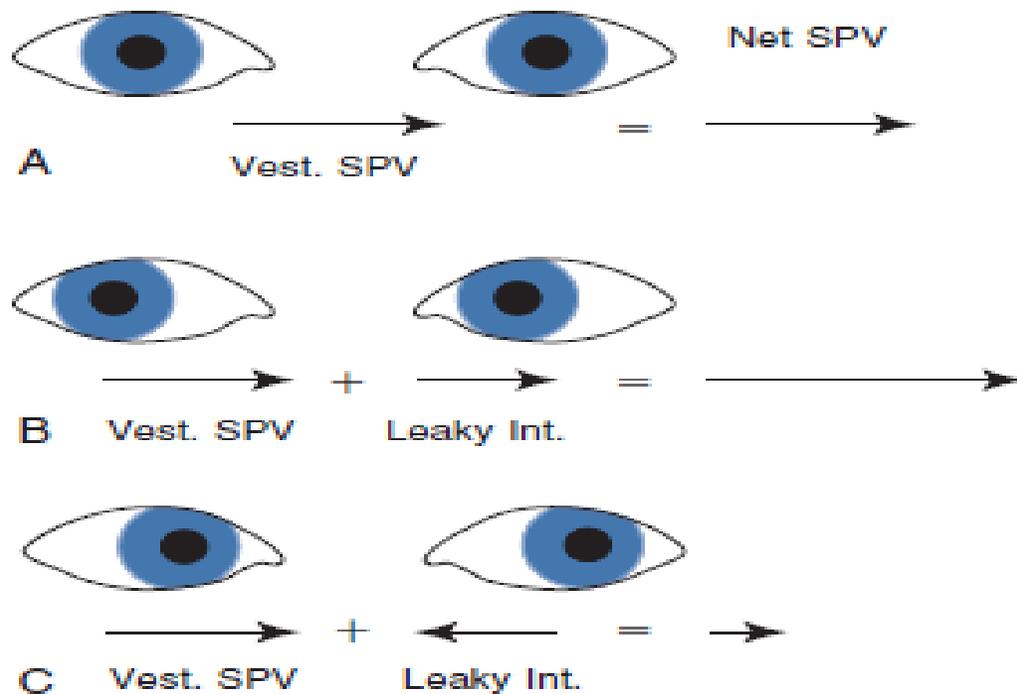


FIGURE 163-29. Alexander's law. The interactions of the vestibular slow-phase velocity (Vest. SPV) and a leaky integrator (Int.) are demonstrated for a case of left acute vestibular hypofunction. In neutral gaze (**A**), the vestibular slow phase alone is manifest. When the gaze is in the direction of the quick phase (*right*, **B**), the leaky integrator causes the eyes to drift to the left. This drift adds to the vestibular slow-phase signal, and the net slow-phase velocity increases. When the gaze is in the direction of the slow phase (*left*, **C**), the leaky integrator causes the eyes to drift to the right. This drift subtracts from the vestibular slow-phase signal, and the net slow-phase velocity decreases.

PRINCIPLE 10: THE UTRICLE SENSES BOTH HEAD TILT AND TRANSLATION, BUT LOSS OF UNILATERAL UTRICULAR FUNCTION IS INTERPRETED BY THE BRAIN AS A HEAD TILT TOWARD THE OPPOSITE SIDE

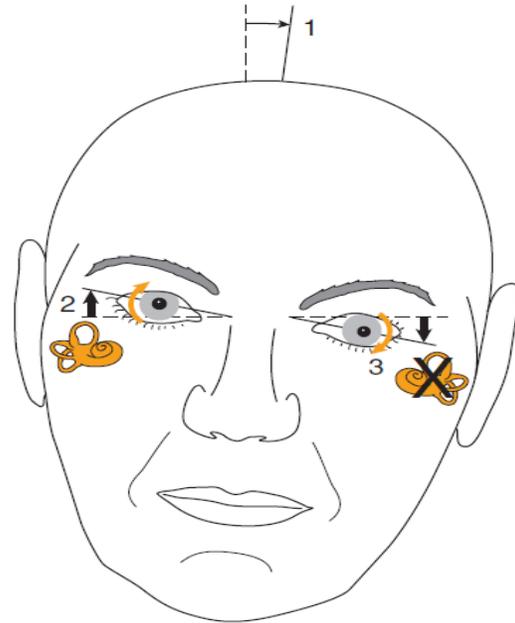


FIGURE 163-30. The otolith tilt reaction for loss of left utricular function consists of 1) head tilt to the left, 2) elevation of the right eye and depression of the left eye, and 3) roll of the superior pole of each eye to the patient's left.

