12

The Vestibular System and Our Sense of Equilibrium

Chapter 12 The Vestibular System and Our Sense of Equilibrium

- Vestibular Contributions to Equilibrium
- Modalities and Qualities of Spatial Orientation
- The Mammalian Vestibular System
- Spatial Orientation Perception
- Sensory Integration
- Active Sensing
- Reflexive Vestibular Responses
- Spatial Orientation Cortex
- When the Vestibular System Goes Bad

Introduction

Vestibular organs: The set of five organs—three semicircular canals and two otolith organs—located in each inner ear that sense head motion and head orientation with respect to gravity.

- Also called the “vestibular labyrinth” or the “vestibular system”

An often overlooked sense:

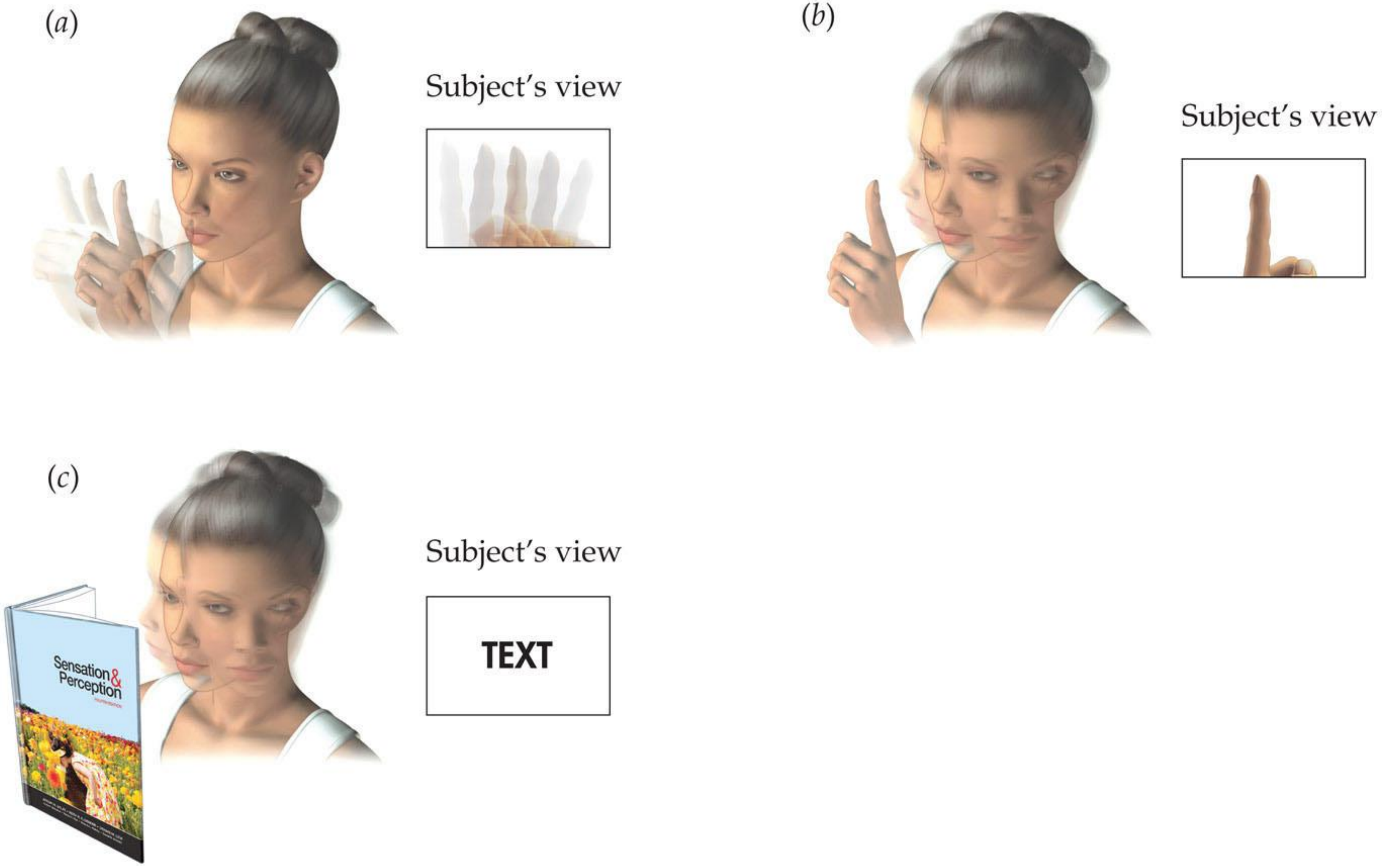
- The vestibular “sixth sense”
- Evolutionarily very old

Introduction

The vestibular organs help us in many ways:

- Provide a sense of spatial orientation, consisting of
  - Linear motion
  - Angular motion
  - Tilt
- Allow for the **vestibulo-ocular reflex**
  - Stabilizes visual input by counterrotating the eyes to compensate for head movement

Figure 12.1 Demonstration of the vestibulo-ocular reflex



SENSATION & PERCEPTION 4e, Figure 12.1

Introduction

Problems with the vestibular system can lead to peculiar sensations:

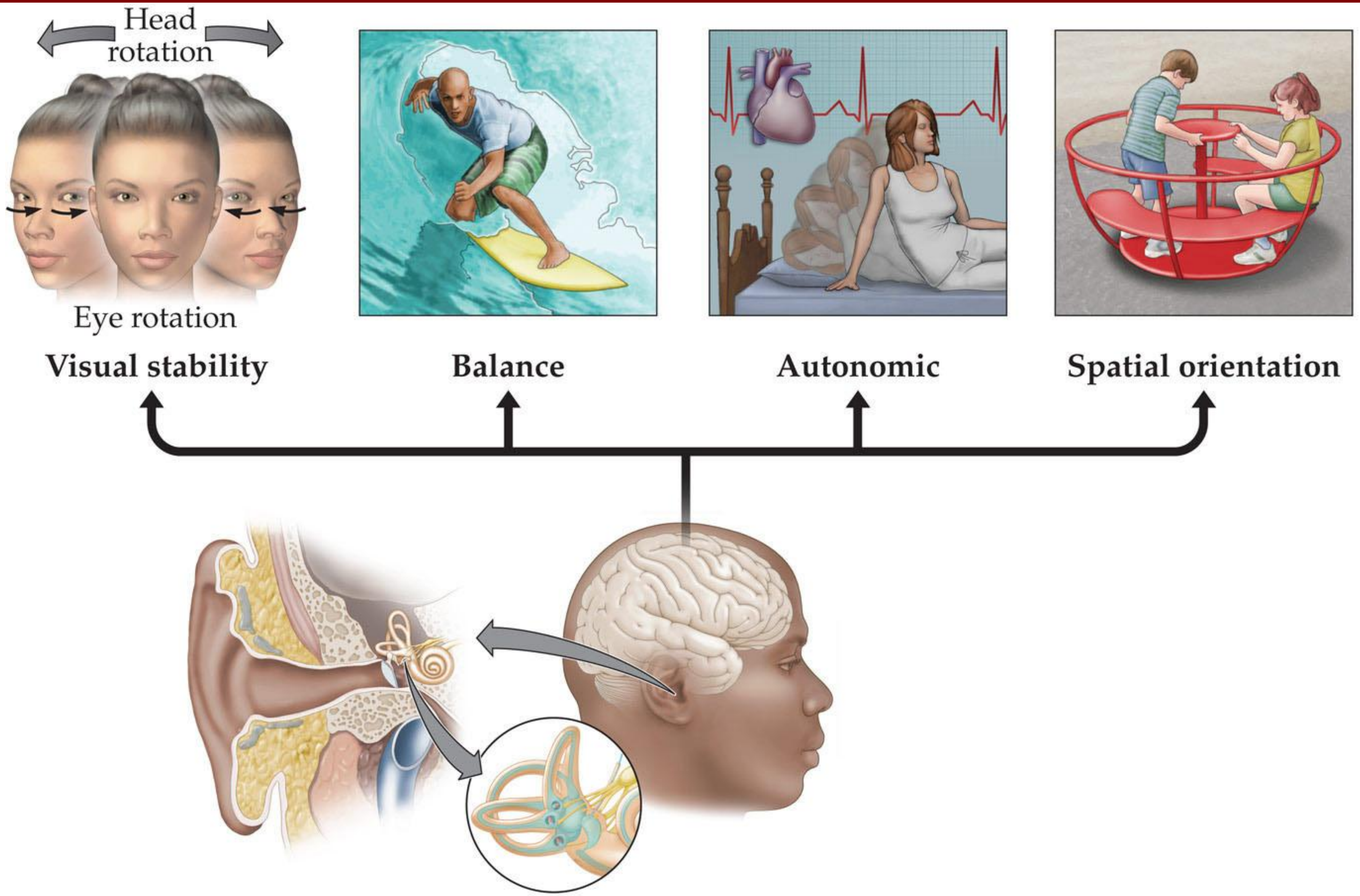
- Spatial Disorientation: Any impairment of spatial orientation (i.e., our sense of linear motion, angular motion, or tilt).
- Dizziness: Nonspecific spatial disorientation.
- Vertigo: A sensation of rotation or spinning.
- Imbalance
- Blurred vision
- Illusory self-motion

Vestibular Contributions to Equilibrium

The vestibular system helps us to maintain our balance and stabilize our eyes during head motion.

- Balance: The neural processes of postural control by which weight is evenly distributed, enabling us to remain upright and stable.

Figure 12.2 Our equilibrium sense is composed of multiple reflexes and multiple perceptual modalities that begin with the vestibular organs in the inner ear



SENSATION & PERCEPTION 4e, Figure 12.2

Vestibular Contributions to Equilibrium

Our sense of equilibrium is active, not passive.

- Active sensing: Sensing that includes self-generated probing of the environment.

Our vestibular sense is continuously integrating both afferent signals and efferent commands.

- Afferent signals: Flow from our senses to our brain.
- Efferent commands: Flow from our brain to our muscles.

Modalities and Qualities of Spatial Orientation

Spatial orientation: A sense consisting of three interacting sensory modalities—perception of linear motion, angular motion, and tilt.

1. Angular motion: Can be sensed when rotating head from side to side as if to say “no.”
2. Linear motion: Sensed when accelerating or decelerating in a car.
3. Tilt: Can be sensed when nodding head up and down as if to say “yes.”

Modalities and Qualities of Spatial Orientation

Why considered different “modalities”?

- Sensing linear motion, angular motion, and tilt involve different receptors and/or different stimulation energy.

Modalities and Qualities of Spatial Orientation

Semicircular canals: The three toroidal tubes in the vestibular system that sense angular acceleration, a change in angular velocity.

- Source of our sense of angular motion, "head spinning" **in pitch, yaw & roll**.

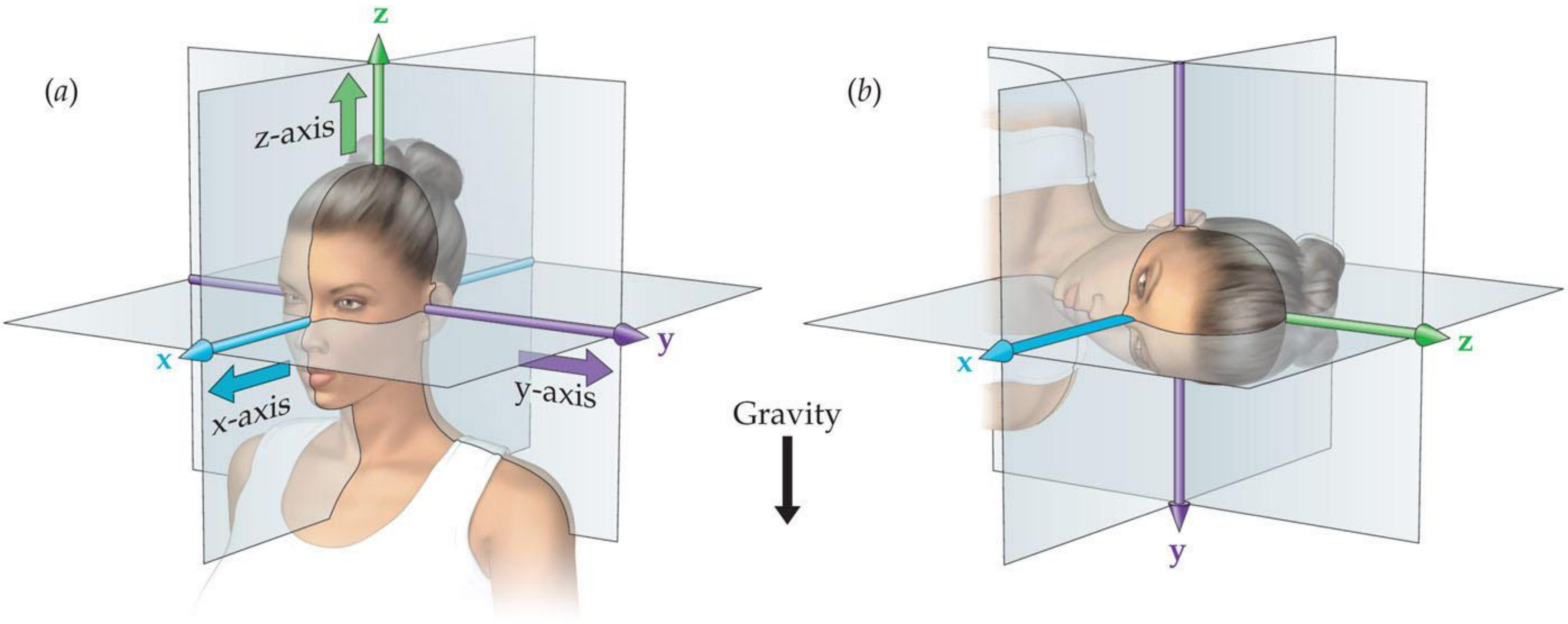
Otolith organs: The mechanical structures in the vestibular system that sense both linear acceleration and gravity.

- Source of our sense of linear velocity and gravity **(up, down, left, right, front, back)**

Coordinate system for classifying direction

- x-axis: Points forward, in the direction the person is facing (roll, “maybe”)
- y-axis: Points laterally, out of the person’s left ear (pitch, “yes”)
- z-axis: Points vertically, out of the top of the head (yaw, “no”)
- Axes are defined relative to the person, not relative to gravity.

Figure 12.3 Movement of the head can be described in terms of a simple fixed coordinate system



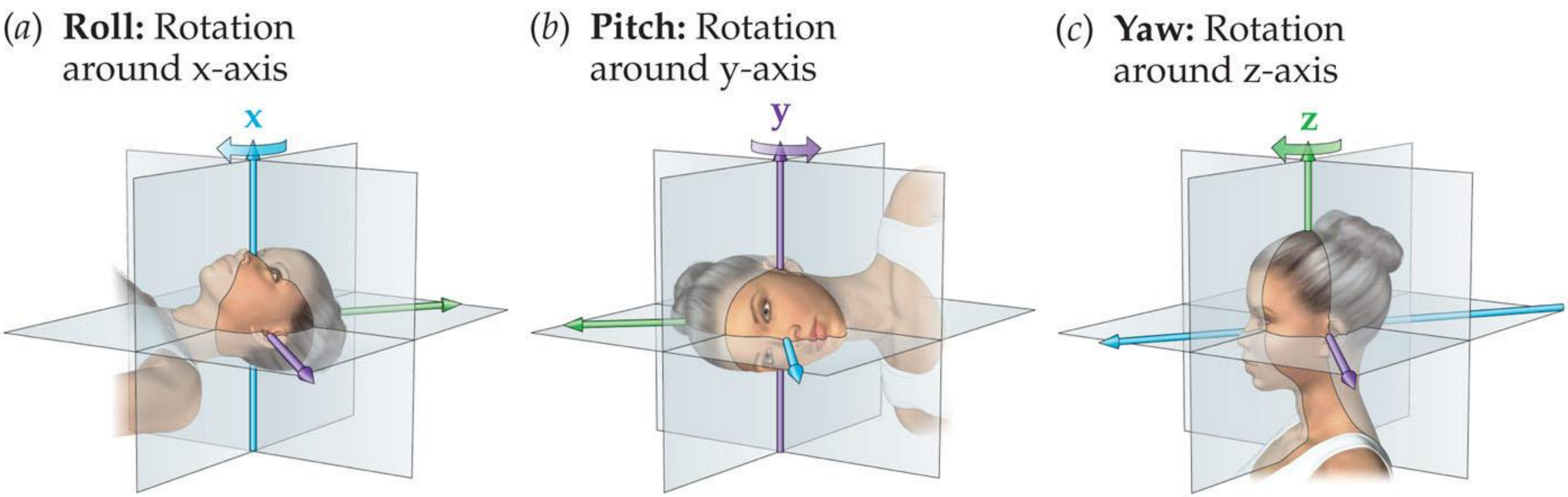
SENSATION & PERCEPTION 4e, Figure 12.3

Modalities and Qualities of Spatial Orientation

Three directions for sense of rotation

- Pitch: Rotation around y-axis – “Yes”
- Yaw: Rotation around z-axis – “No”
- Roll: Rotation around x-axis – **“Maybe, maybe not”**

Figure 12.4 Rotating bodies can move in three directions



SENSATION & PERCEPTION 4e, **Figure 12.4**

Modalities and Qualities of Spatial Orientation

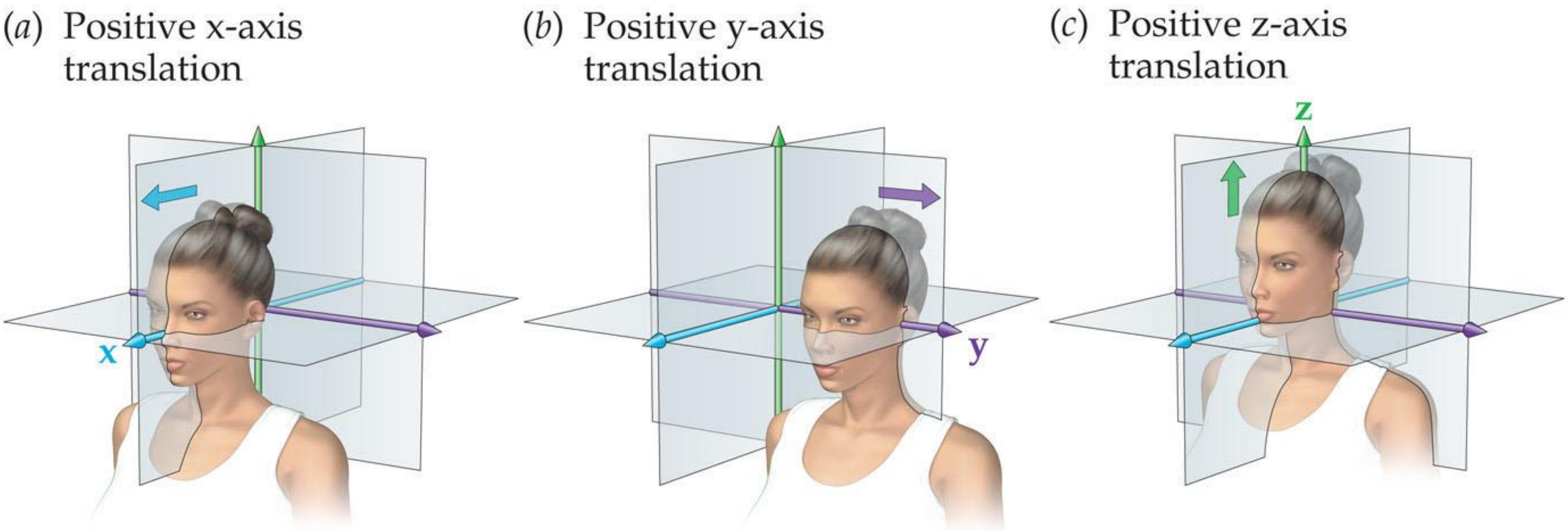
Each spatial orientation modality can change in terms of its amplitude and direction.

- Amplitude: The size (increase or decrease) of a head movement (e.g., angular velocity, linear acceleration, tilt).
- Direction: The line one moves along or faces, with reference to the point or region one is moving toward or facing.

Linear motion

- Movements represented in terms of changes in the x-, y-, and z-axes
- Any arbitrary linear motion can be represented as a change along these three axes.

Figure 12.5 Translating bodies can move in three directions



SENSATION & PERCEPTION 4e, Figure 12.5

The Mammalian Vestibular System

The vestibular organs do not respond to constant velocity.

- They only respond to changes in velocity—acceleration.

Gravity and acceleration share a deep connection and can be considered equivalent.

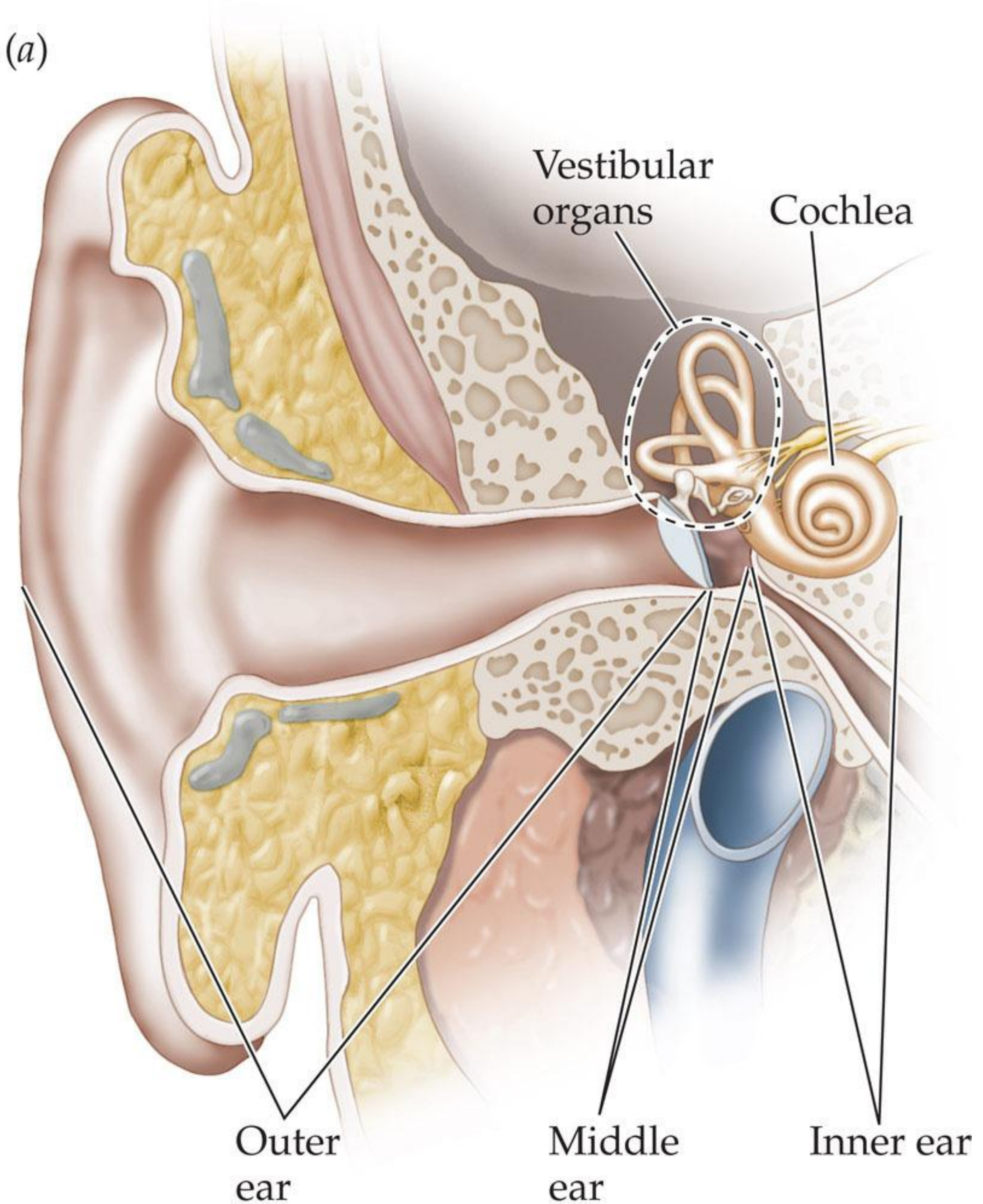
Hair cell: Any cell that has stereocilia for transducing mechanical movement in the inner ear into neural activity sent to the brain.

Mechanoreceptor: A sensory receptor that is responsive to mechanical stimulation (pressure, vibration, or movement).

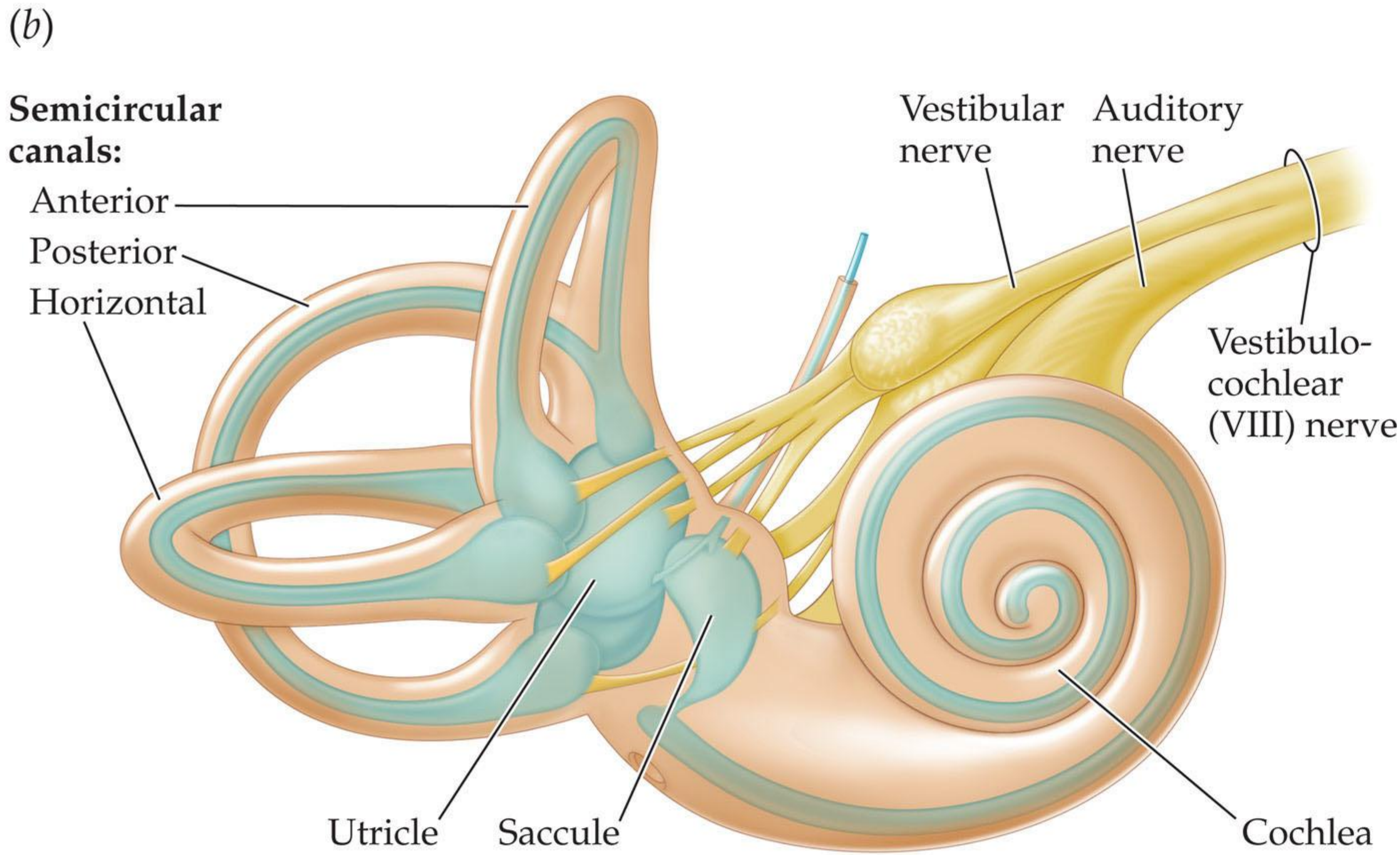
Like the hair cells involved in hearing, hair cells act as the mechanoreceptors in each of the five vestibular organs.

Head motion causes hair cell **stereocilia** to deflect, causing a change in hair cell voltage and altering neurotransmitter release.

Figure 12.7 The vestibular organs (Part 1)



SENSATION & PERCEPTION 4e, Figure 12.7 (Part 1)



SENSATION & PERCEPTION 4e, Figure 12.7 (Part 2)

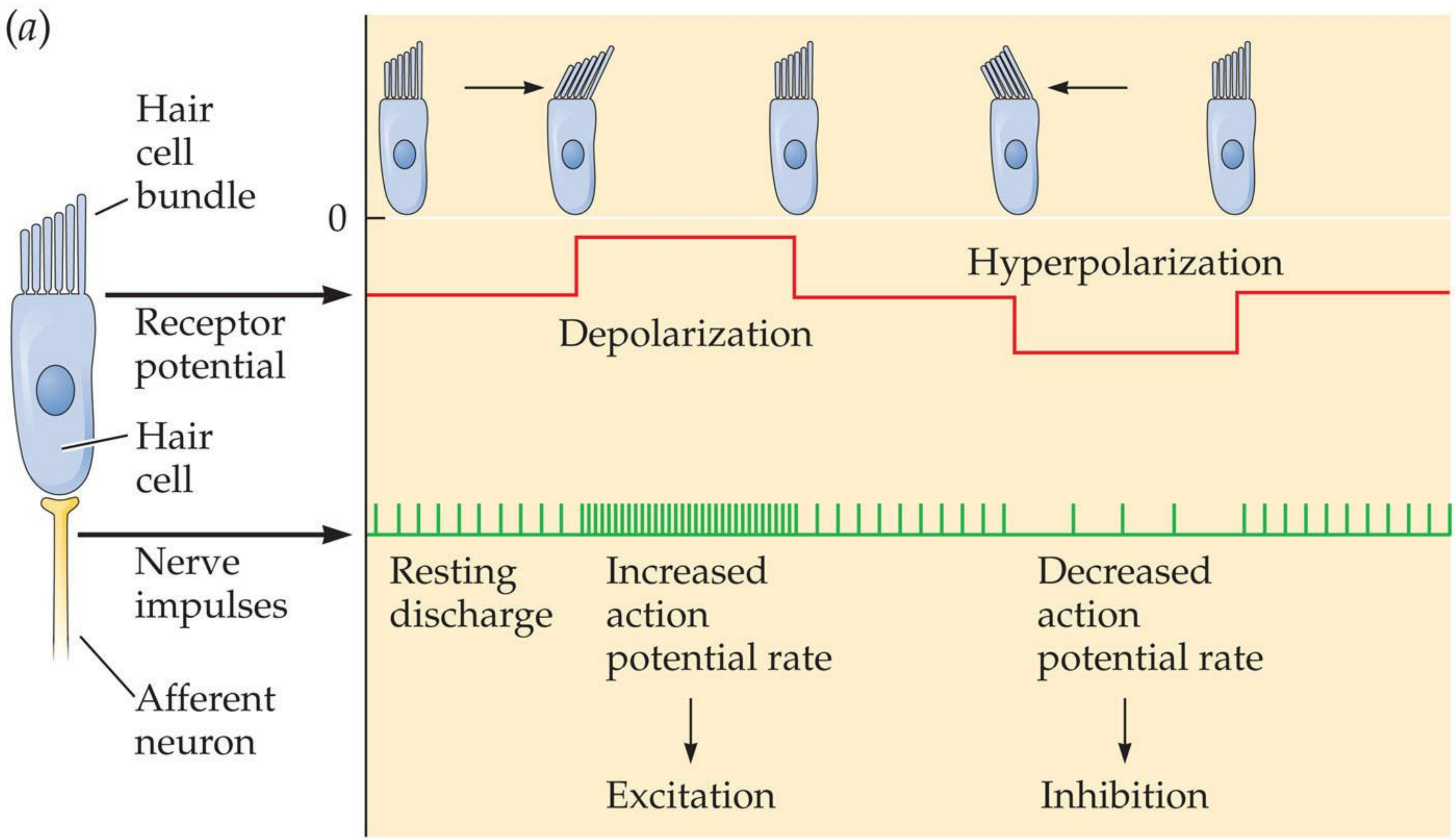
Hair cell responses

- In the absence of stimulation, hair cells release neurotransmitter at a constant rate.
- When hair cell bundles bend, the change in hair cell voltage is proportional to the amount of deflection.
    - Bending **toward** tallest stereocilia (kinocilia): **depolarization**
    - Bending **away** from tallest stereocilia: **hyperpolarization**

Hair cell responses (*continued*)

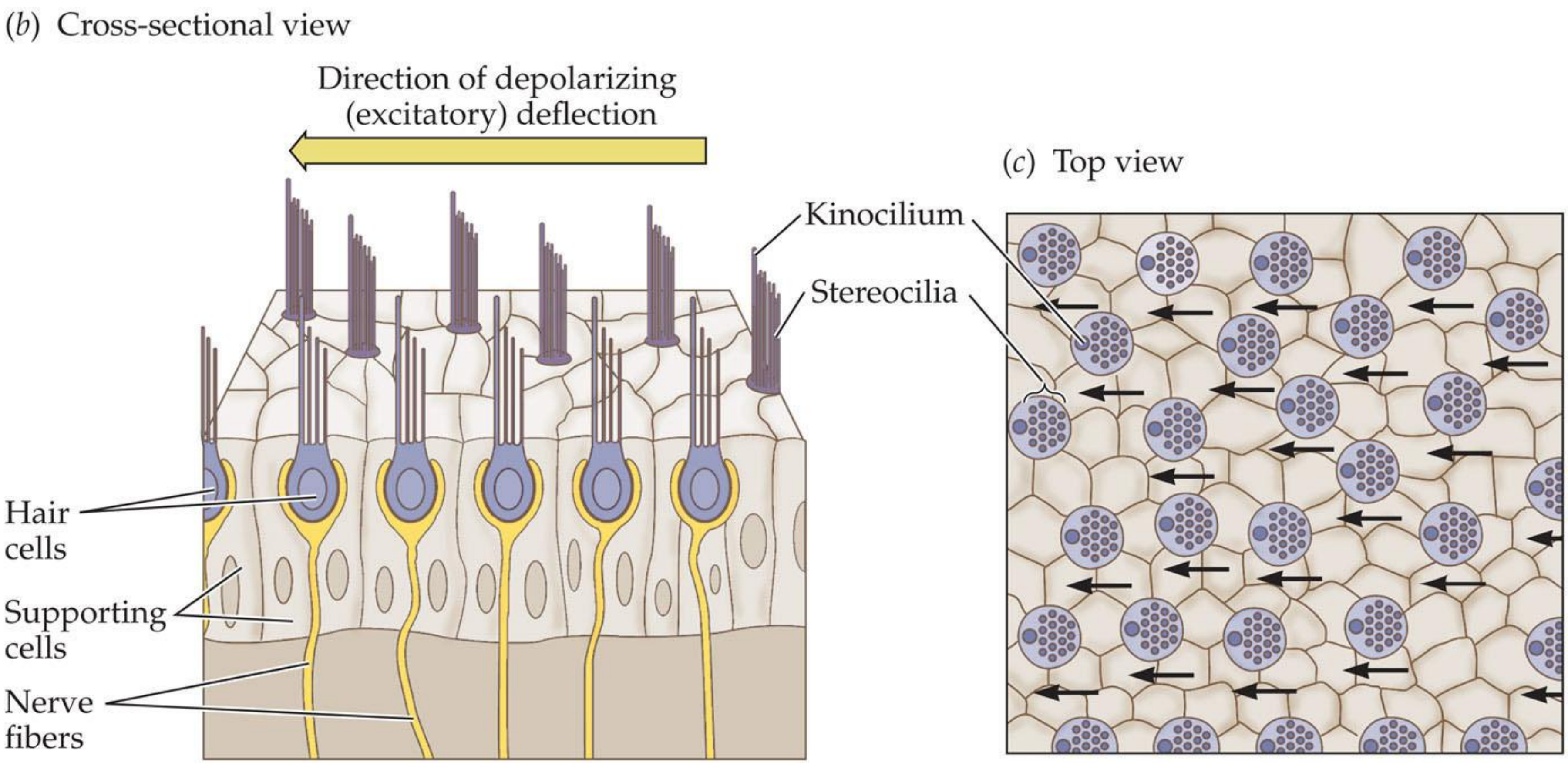
- Hair cells increase firing to rotation in one direction and decrease firing to rotation in the opposite direction.

Figure 12.8 Hair cell responses (Part 1)



SENSATION & PERCEPTION 4e, Figure 12.8 (Part 1)

Figure 12.8 Hair cell responses (Part 2)



SENSATION & PERCEPTION 4e, Figure 12.8 (Part 2)

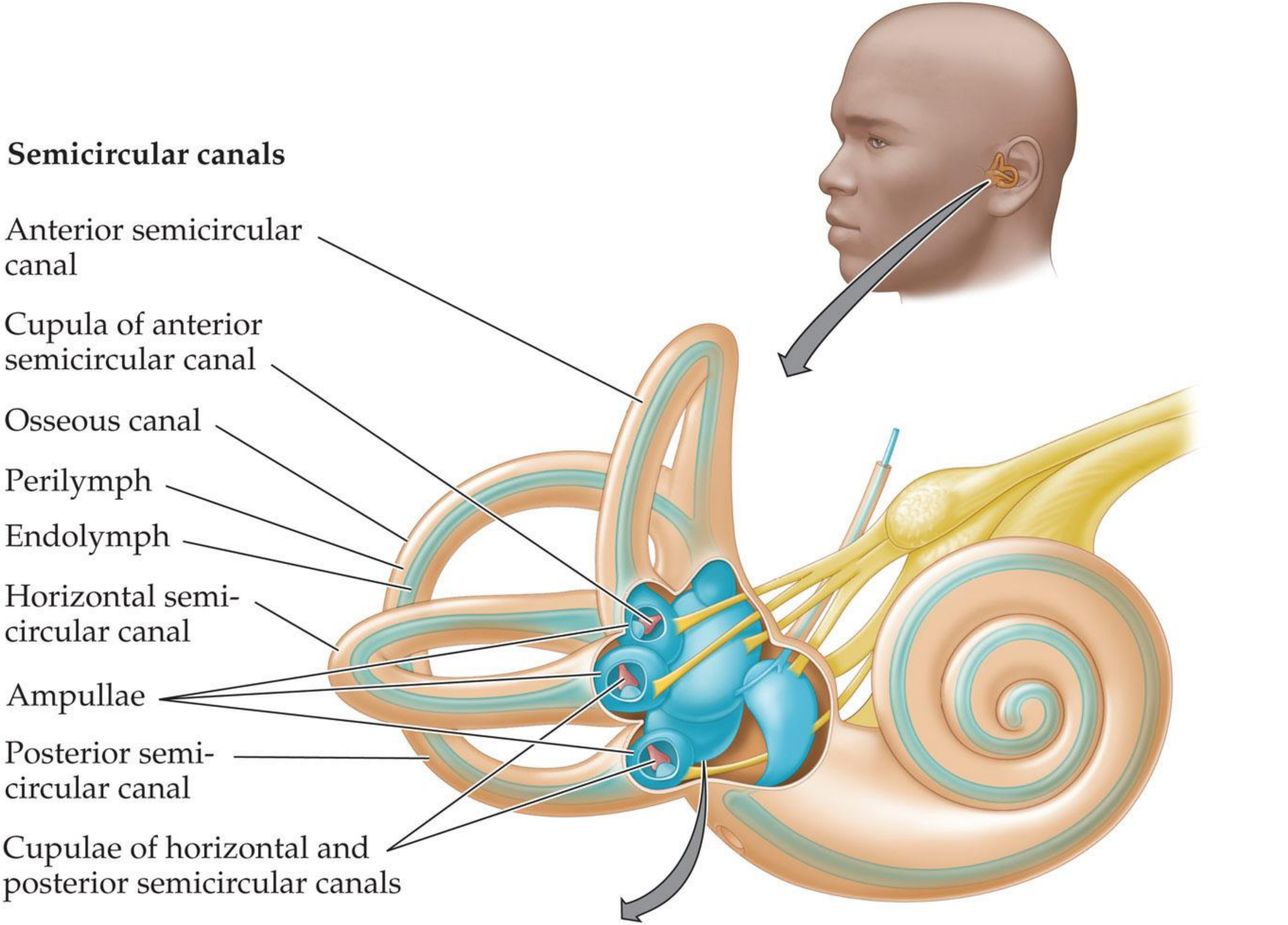
Semicircular canals

- Each one is about three-fourths of a toroid (donut) shape, measuring 15 mm long and 1.5 mm in diameter.
  - Canals are filled with a fluid called perilymph.
- A second, smaller toroid is found inside the larger toroid, measuring 0.3 mm in diameter.
  - Formed by a membrane filled with fluid called endolymph

Semicircular canals (*continued*)

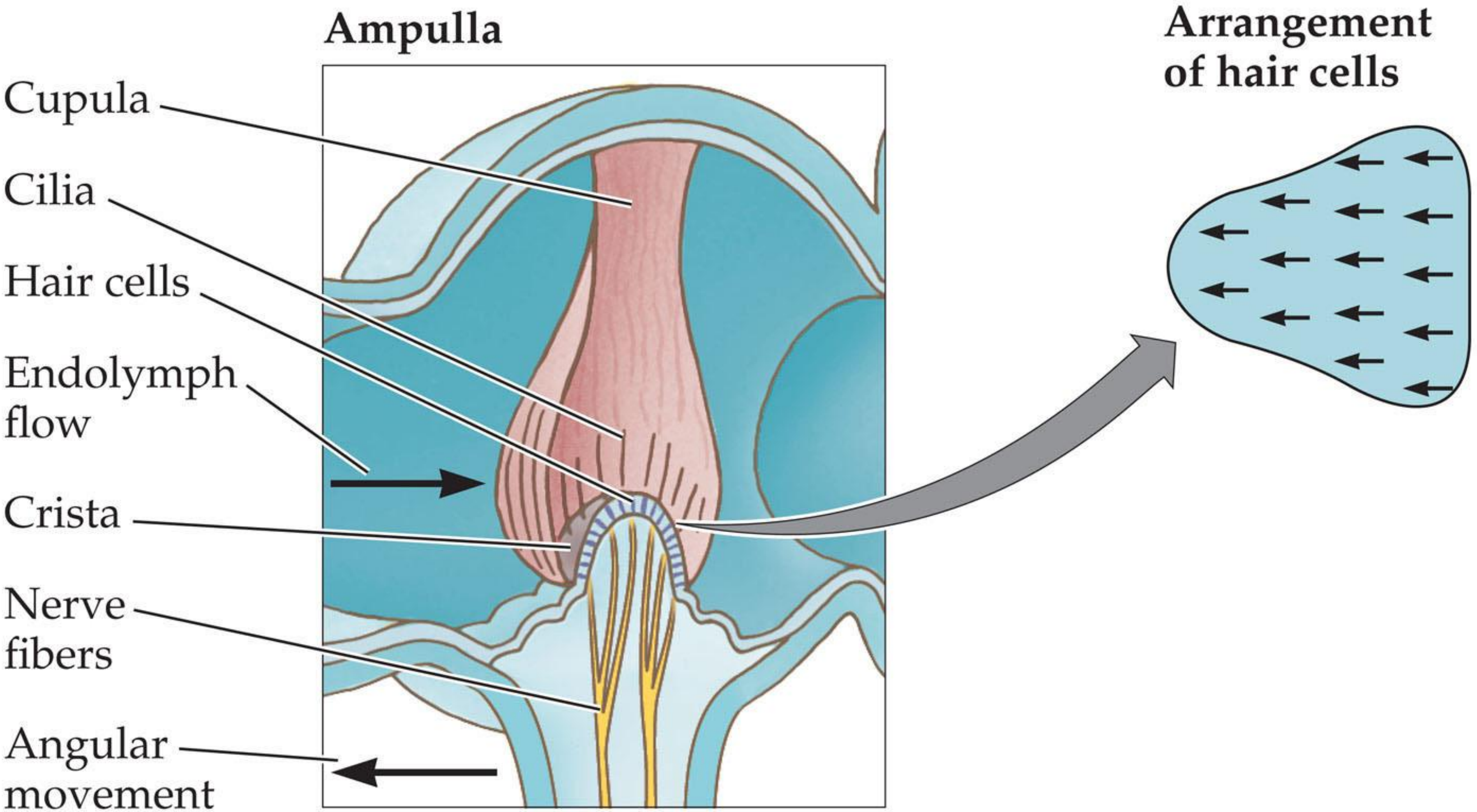
- Cross section of each canal swells substantially near where the canals join the vestibule.
  - Ampulla: An expansion of each semicircular-canal duct that includes that canal’s cupula, crista, and hair cells, where transduction occurs.

Figure 12.9 The semicircular canals (Part 1)



SENSATION & PERCEPTION 4e, **Figure 12.9 (Part 1)**

Figure 12.9 The semicircular canals (Part 2)



SENSATION & PERCEPTION 4e, Figure 12.9 (Part 2)

Semicircular canals (*continued)*

- Within the endolymph space of each ampulla is the crista.
- Crista: Any of the specialized detectors of angular motion located in each semicircular canal in a swelling called the ampulla.
  - Each crista has about 7000 hair cells, associated supporting cells, and nerve fibers.

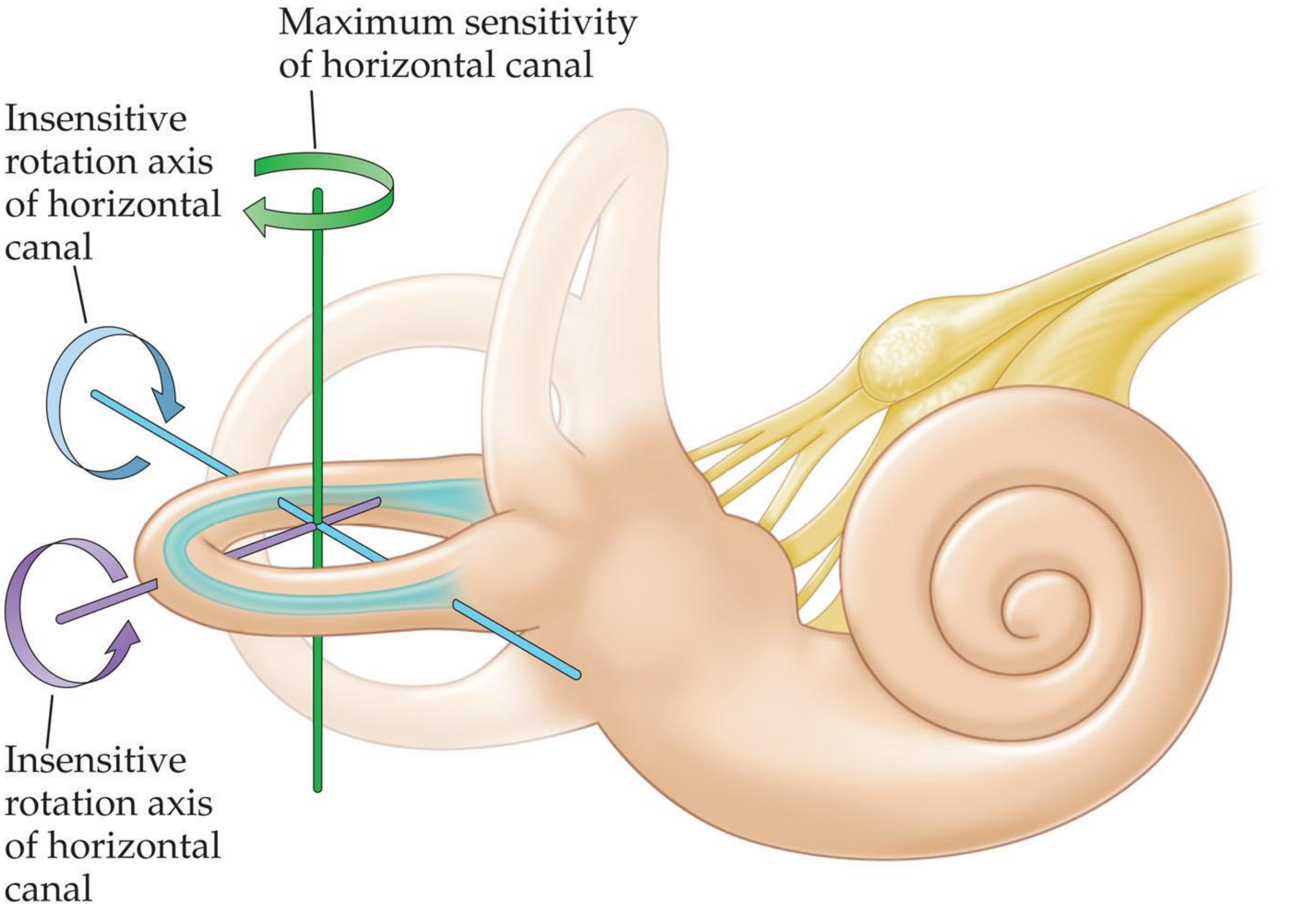
Semicircular canals (*continued)*

- Crista:
    - Cilia of hair cells project into jellylike cupula forming an elastic dam to the opposite ampulla wall, with endolymph on both sides of dam.
- When the head rotates, the inertia of the endolymph causes it to lag behind, leading to tiny deflections of the hair cells.

Coding of direction in the semicircular canals

- Three semicircular canals in each ear
- Each canal is oriented in a different plane.
- Each canal is maximally sensitive to rotations perpendicular to the canal plane.

Figure 12.10 Each semicircular canal is maximally sensitive to rotations perpendicular to the canal plane

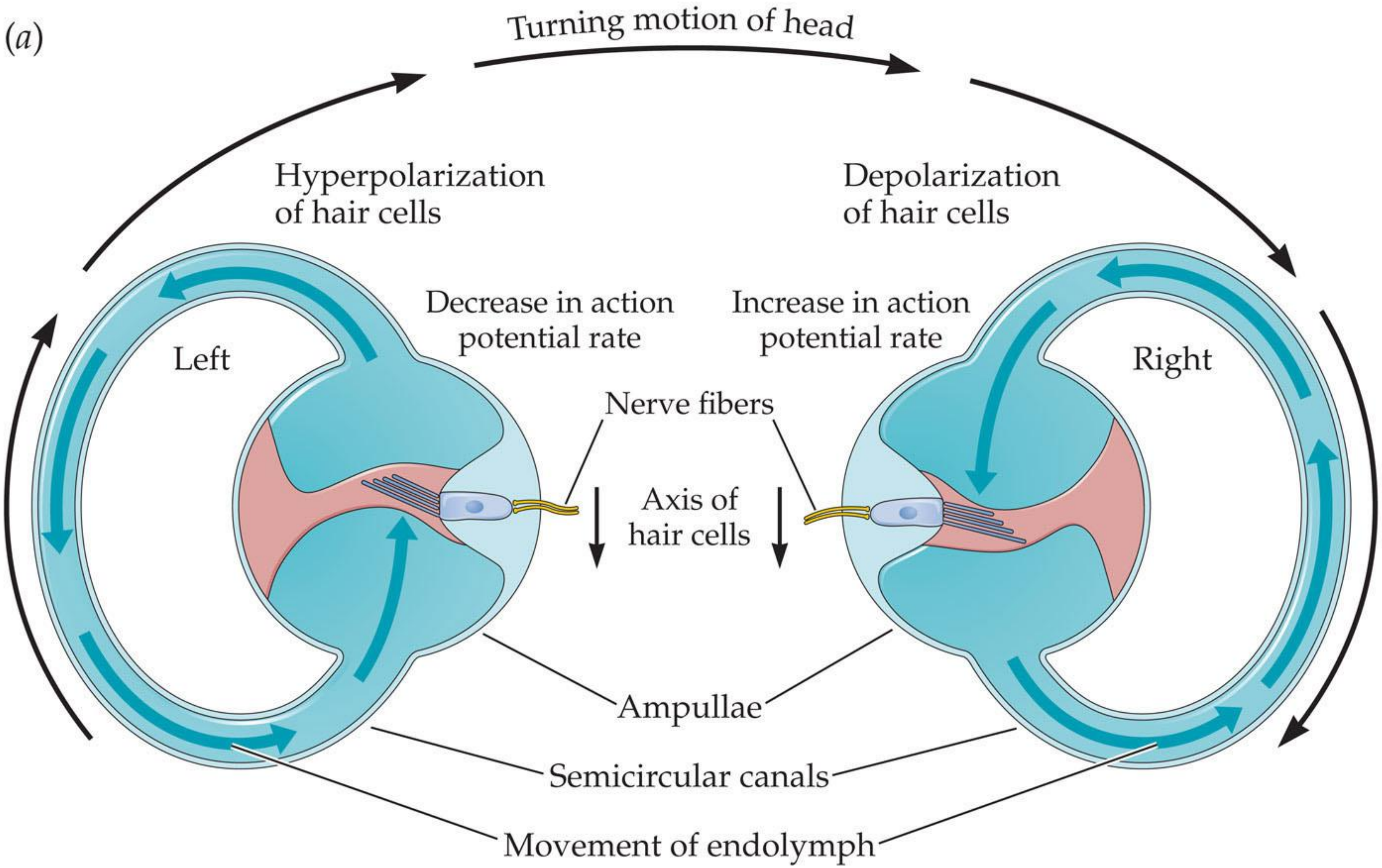


SENSATION & PERCEPTION 4e, Figure 12.10

Push–pull symmetry

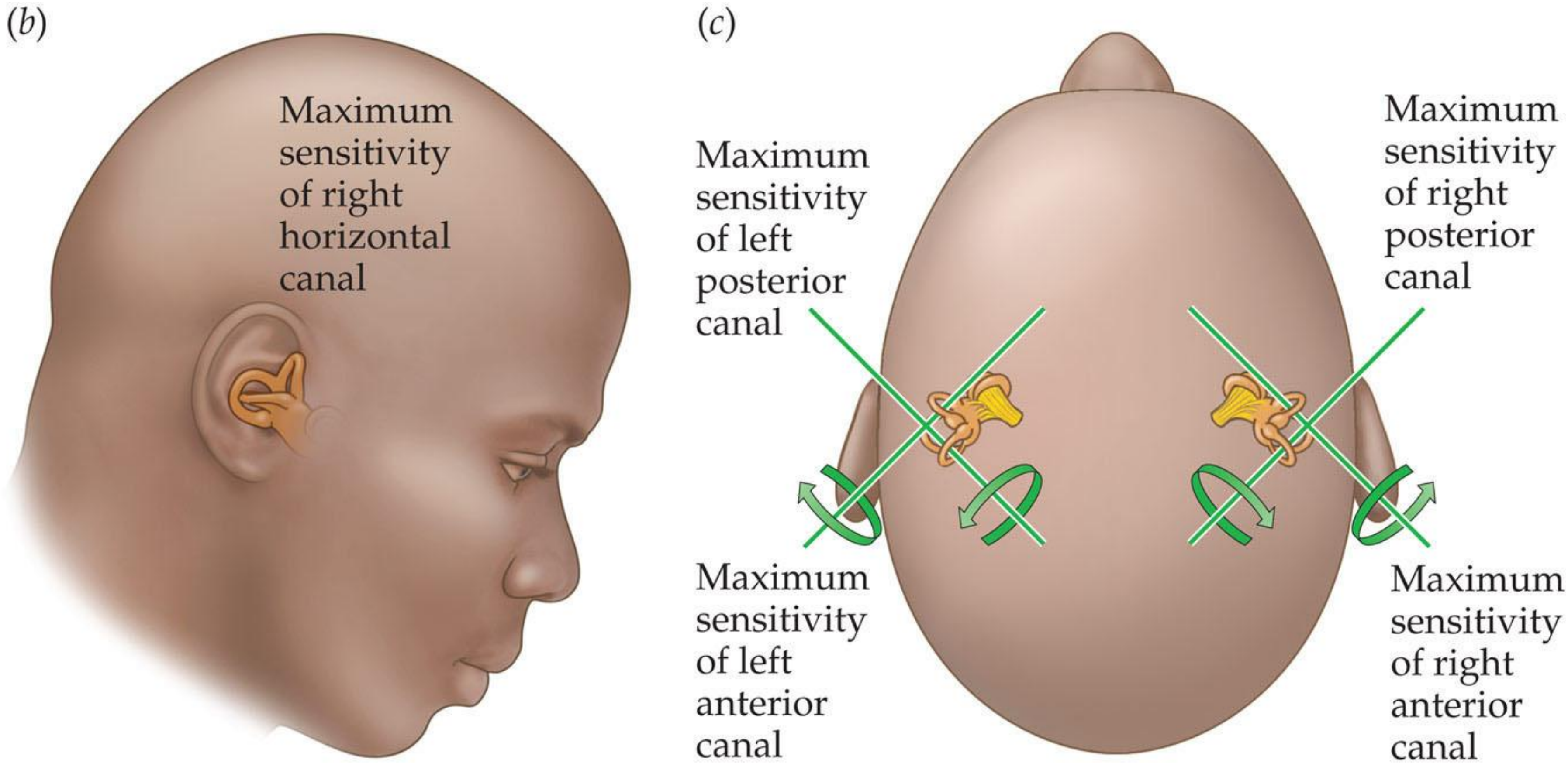
- Hair cells in opposite ears respond in a complementary fashion to each other.
- When hair cells in the left ear depolarize, those in the analogous structure in the right ear hyperpolarize.

Figure 12.11 The semicircular canals function in pairs that have a push-pull relationship (Part 1)



***SENSATION & PERCEPTION 4e*, Figure 12.11 (Part 1)**

Figure 12.11 The semicircular canals function in pairs that have a push-pull relationship (Part 2)



SENSATION & PERCEPTION 4e, Figure 12.11 (Part 2)

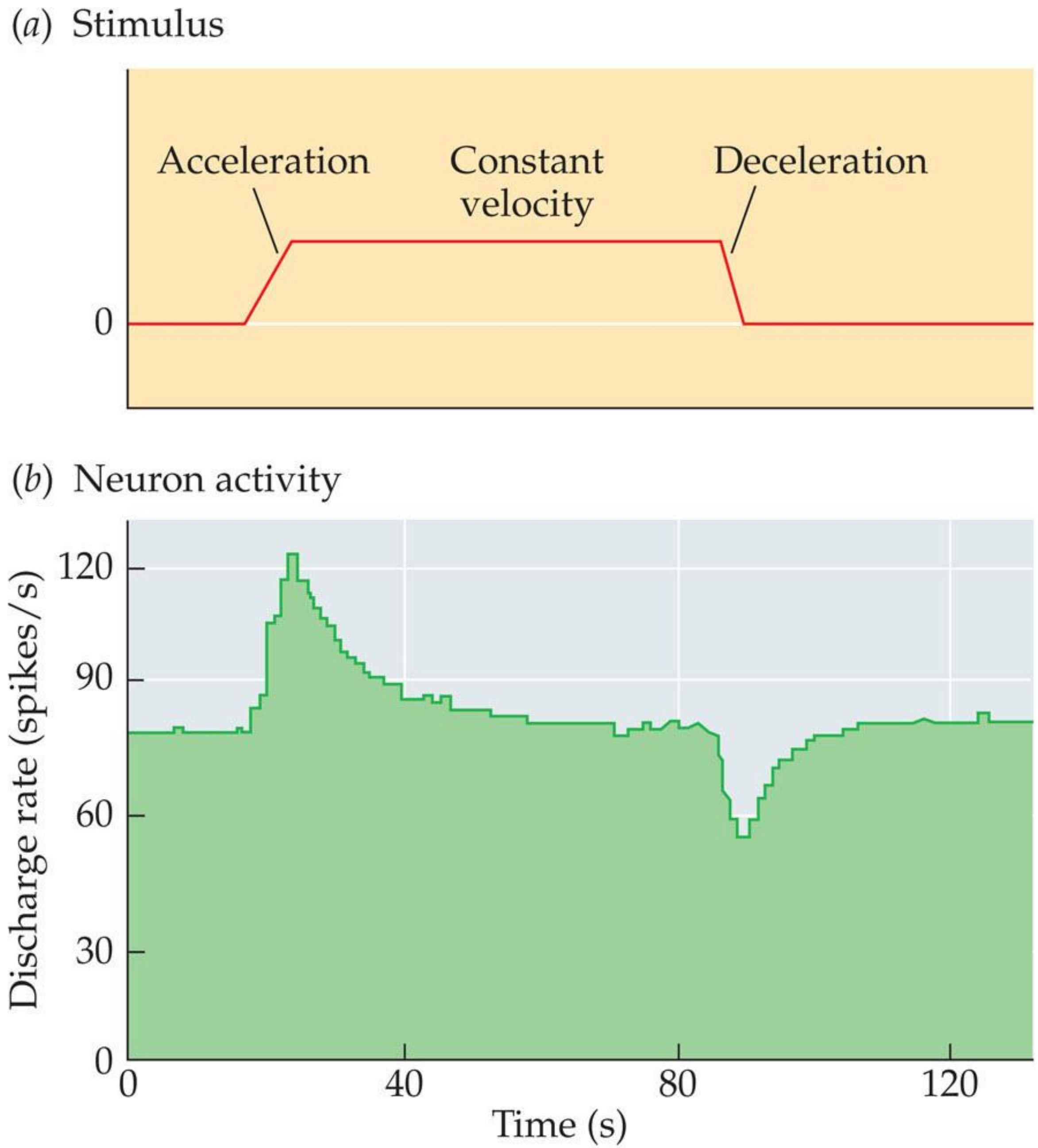
Coding of amplitude in the semicircular canals

- In the absence of any rotation, many afferent neurons from the semicircular canals have a resting firing rate of about 100 spikes/s.
  - This firing rate is high relative to nerve fibers in other sensory systems.
  - High firing rate allows canal neurons to code amplitude by decreasing their firing rate, as well as increasing it.
- Changes in firing rate are proportional to angular velocity of the head aligned with the canal the neuron is in.

Semicircular canal dynamics

- Neural activity in semicircular canals is sensitive to changes in rotation velocity.
- Constant rotation leads to decreased responding from the canal neurons after a few seconds.

Figure 12.12 Response of a semicircular-canal neuron to constant-velocity rotation

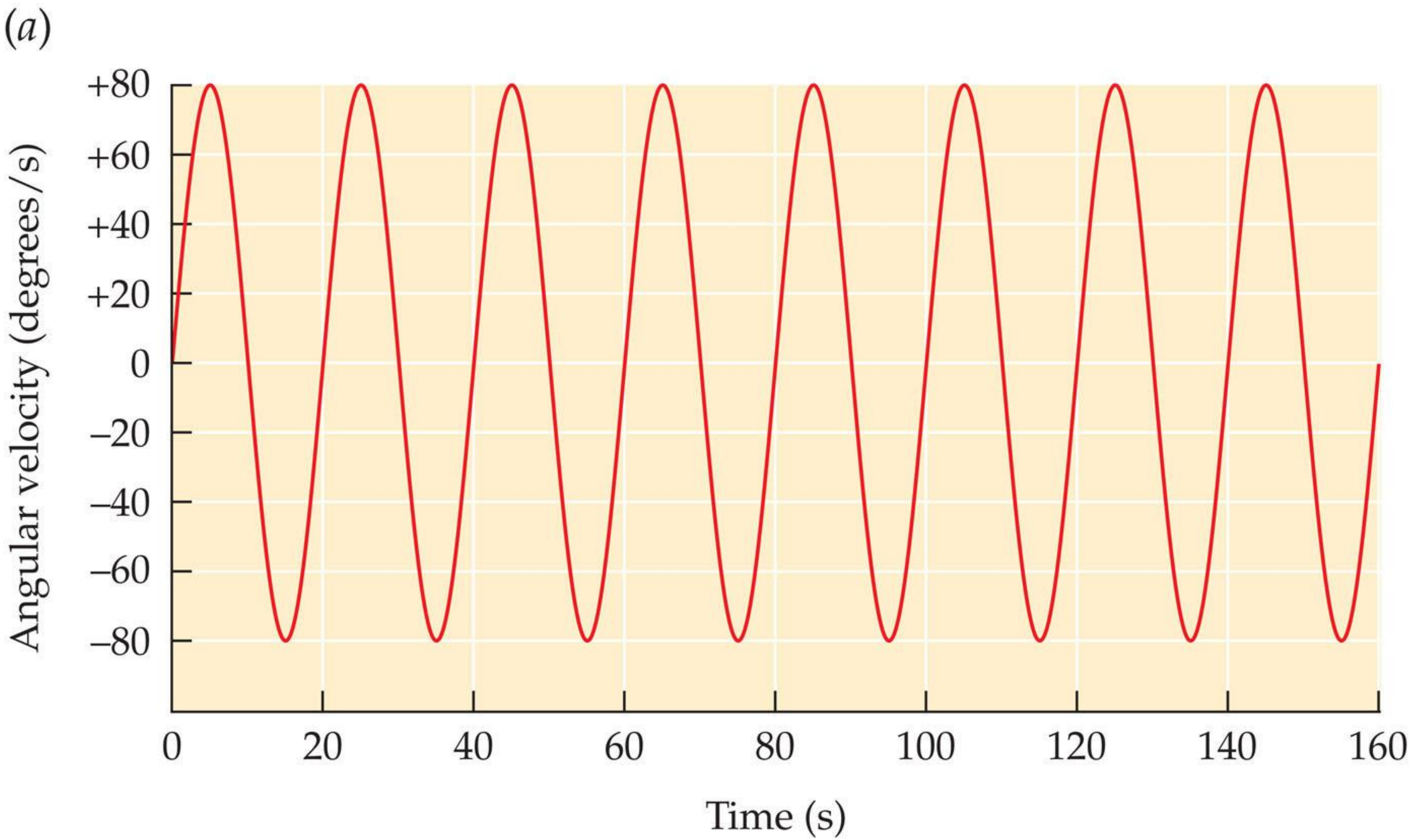


SENSATION & PERCEPTION 4e, Figure 12.12

Semicircular canal dynamics (*continued*)

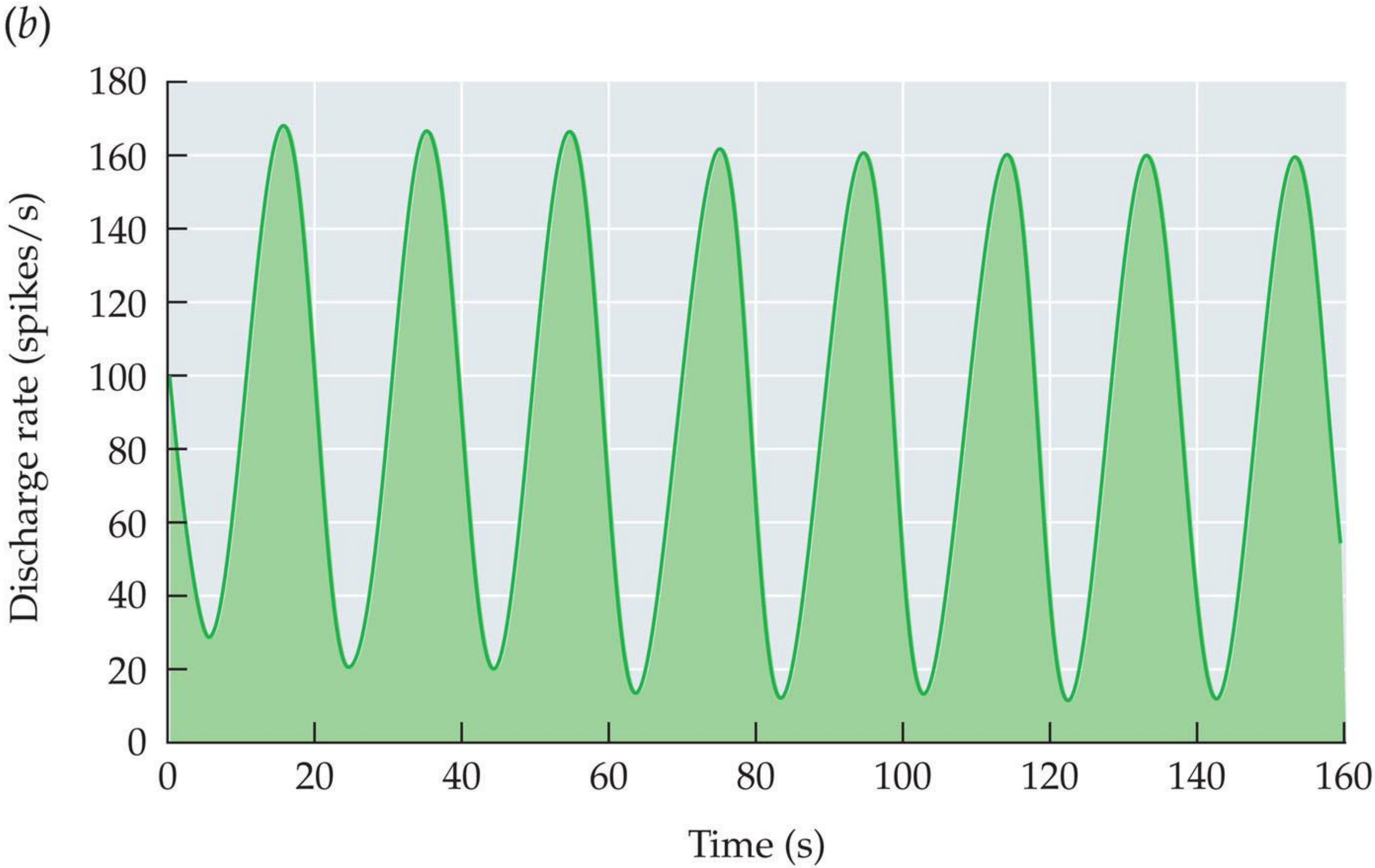
- Canal afferent neurons are sensitive to back and forth rotations of the head, as well.
- Greatest sensitivity to rotations at 1 Hz or less
  - Rotations faster than 1 Hz would be dangerous.
- Firing rate goes up and down as the head rotates back and forth.
- The overall normalized amplitude of the canal neuron response scales with head rotation frequency.

Figure 12.13 Sinusoidal motion trajectories (Part 1)



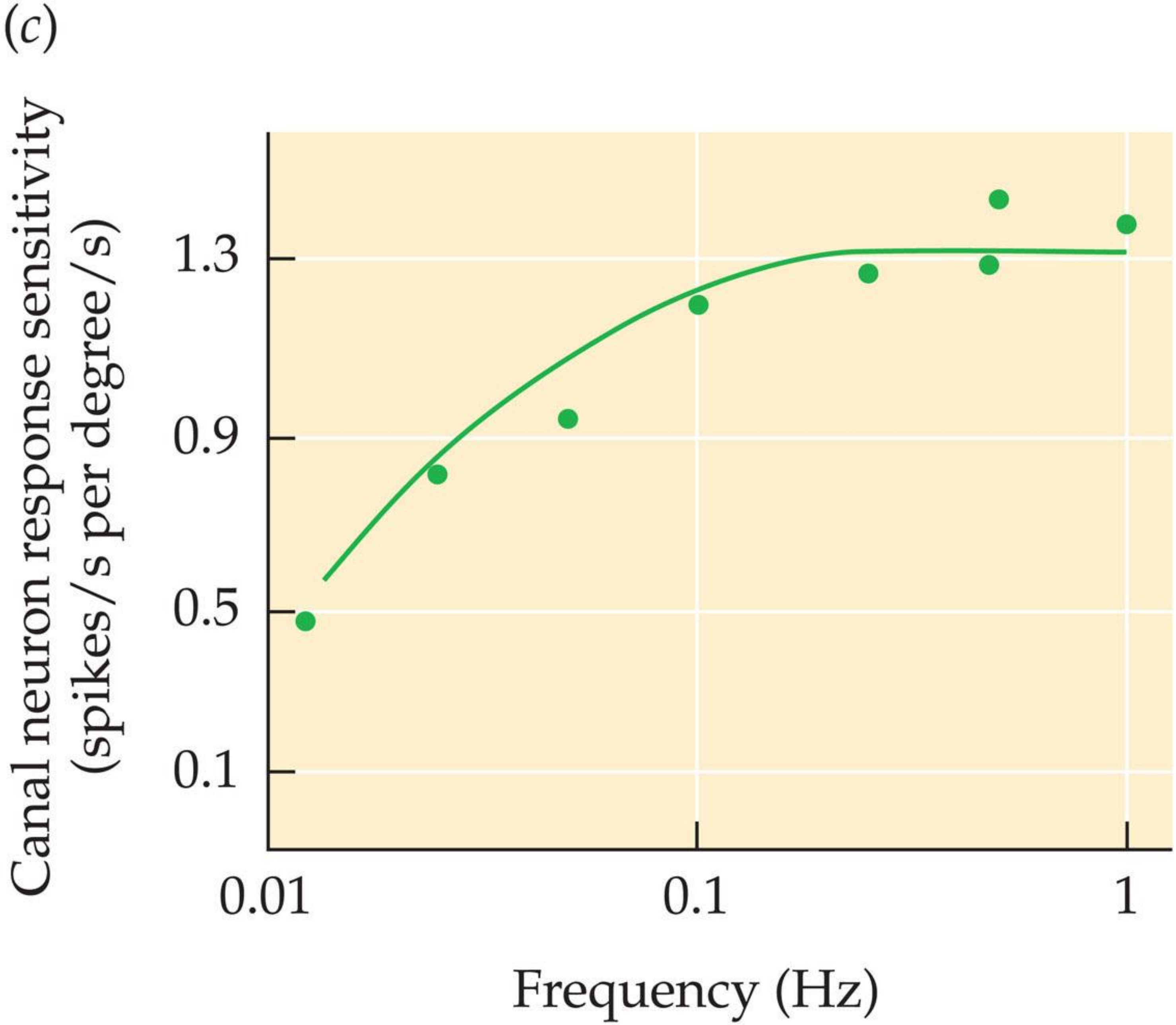
SENSATION & PERCEPTION 4e, Figure 12.13 (Part 1)

Figure 12.13 Sinusoidal motion trajectories (Part 2)



SENSATION & PERCEPTION 4e, **Figure 12.13 (Part 2)**

Figure 12.13 Sinusoidal motion trajectories (Part 3)



SENSATION & PERCEPTION 4e, Figure 12.13 (Part 3)

Why sine wave motions?

- Fourier analysis: Complex motion trajectories can be broken down into simple sine wave motions at different frequencies.
- If we know the responses to single sine wave frequencies, we know a good deal about complex motion perception.

Otolith organs sense acceleration and tilt.

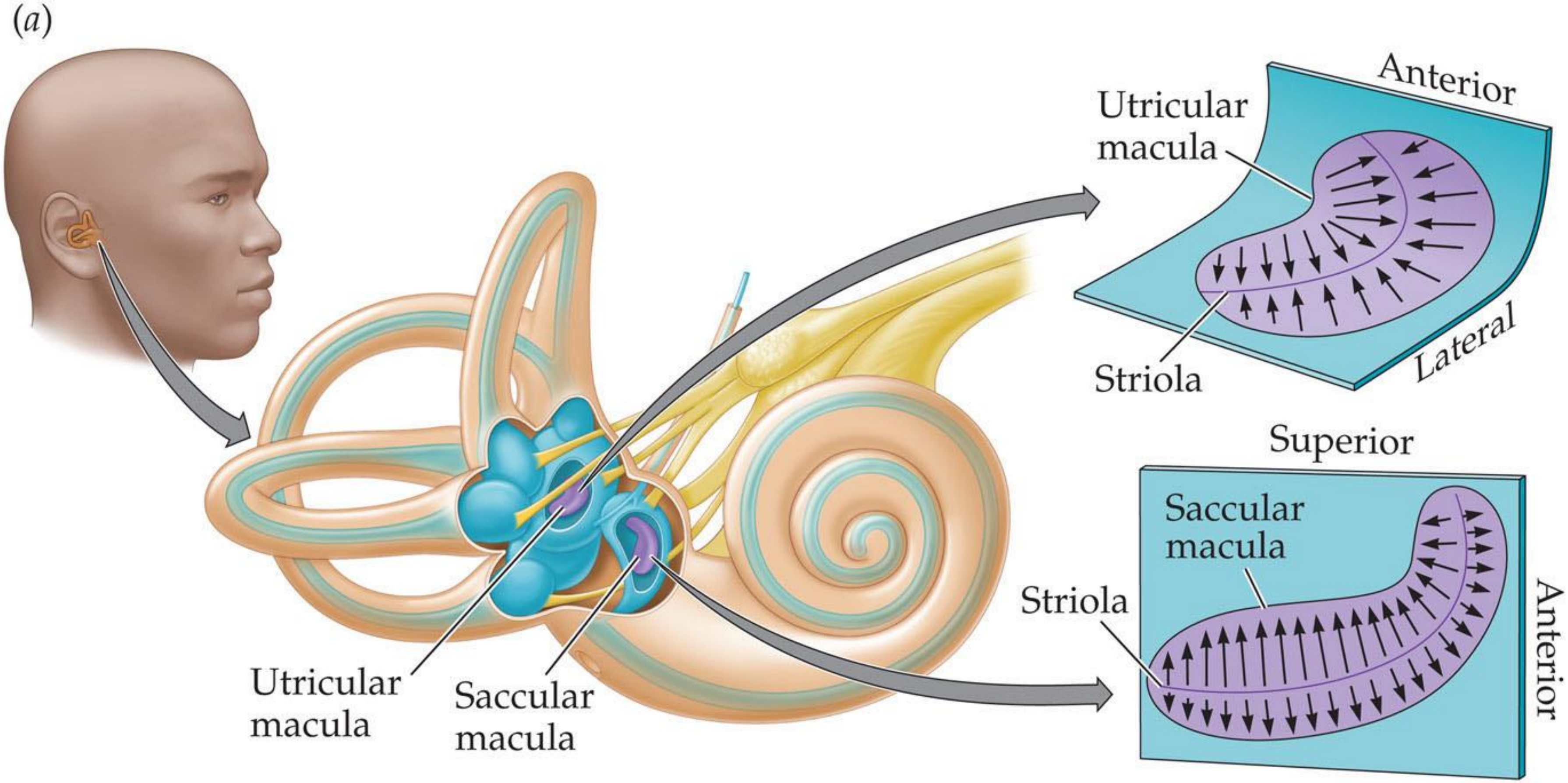
- Two otolith organs in each ear:
  - Utricle: Contains about 30,000 hair cells.
  - Saccule: Contains about 16,000 hair cells.
- Each organ contains a macula: A specialized detector of linear acceleration and gravity.

The Mammalian Vestibular System

Each macula is roughly planar and sensitive primarily to shear forces.

Hair cells are encased in a gelatinous structure that contains calcium carbonate crystals called otoconia ("ear stones" in Greek).

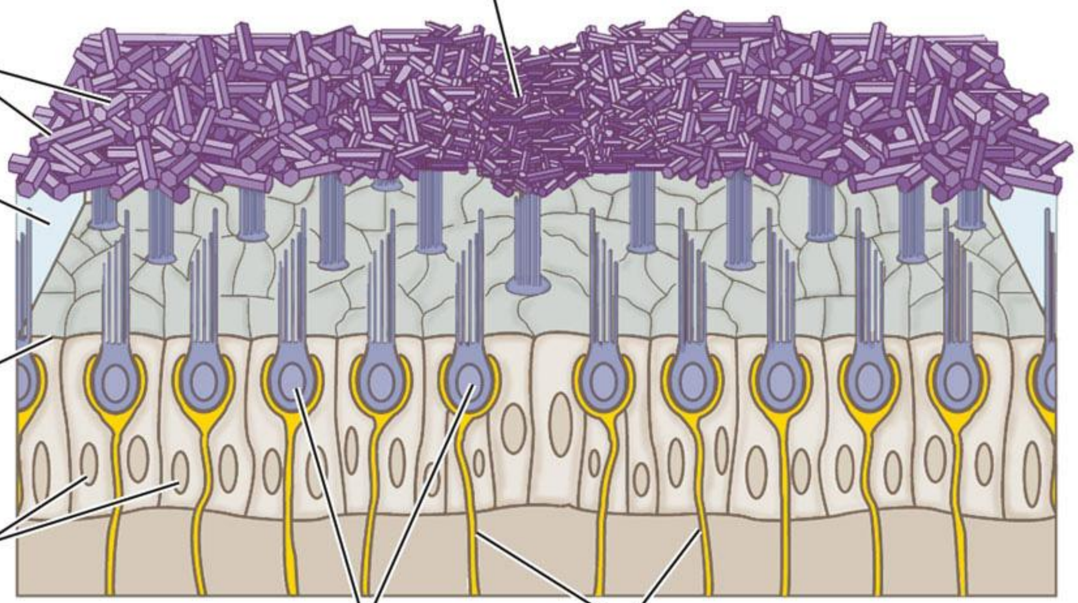
Figure 12.14 The otolith organs (Part 1)



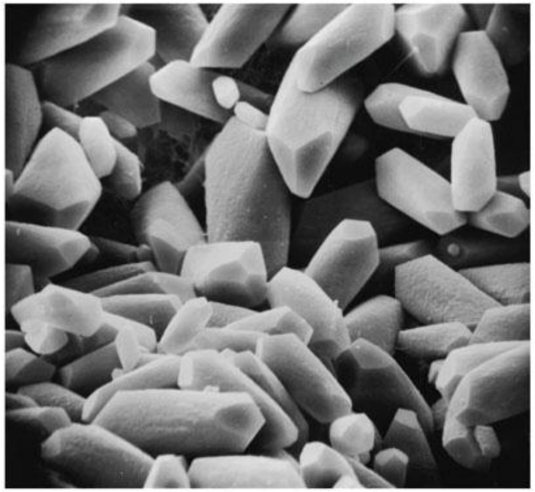
***SENSATION & PERCEPTION 4e,* Figure 12.14 (Part 1)**

Figure 12.14 The otolith organs (Part 2)

(*b*)



(*c*)

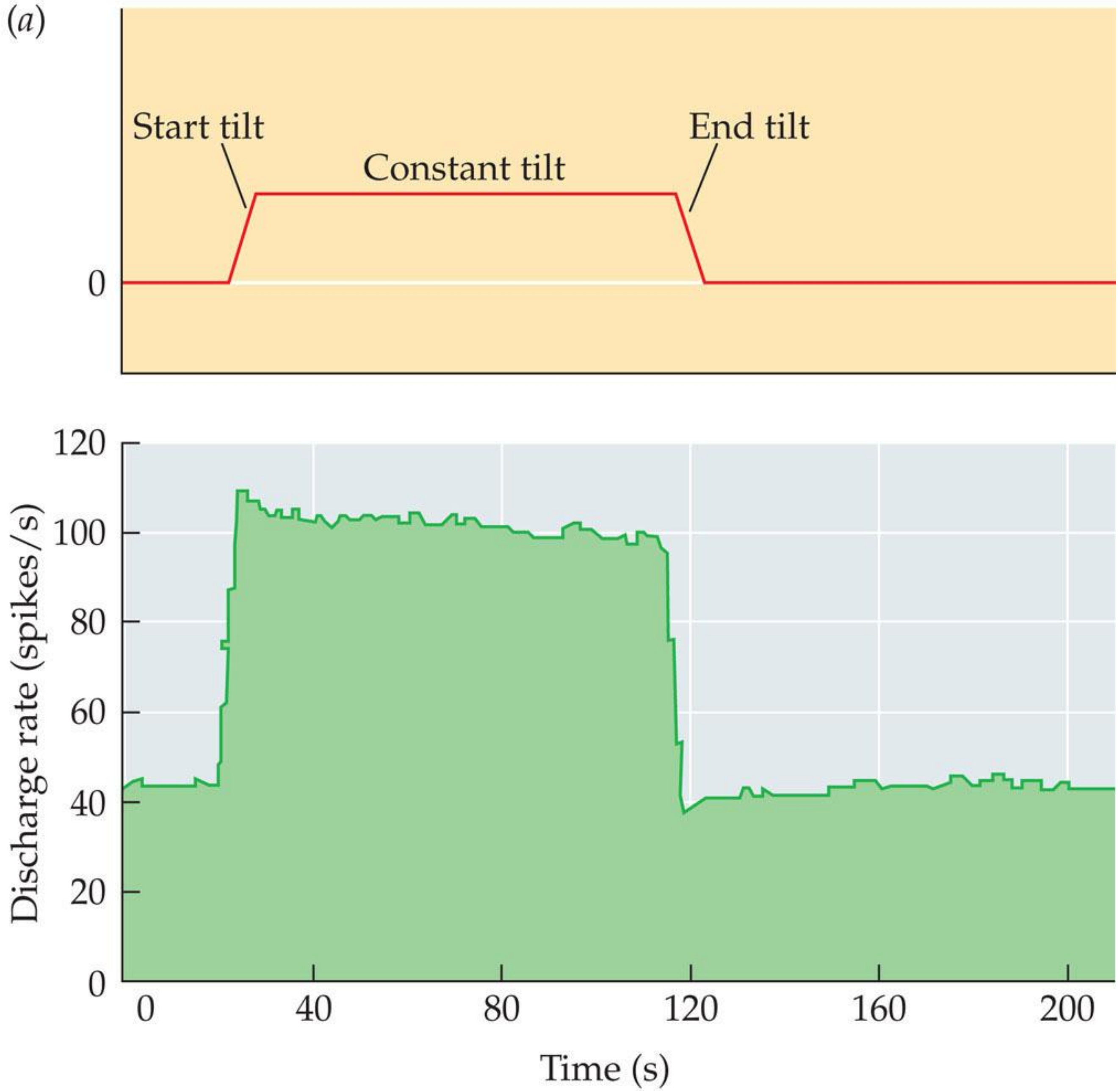


***SENSATION & PERCEPTION 4e*, Figure 12.14 (Part 2)**

Coding of amplitude in the otolith organs

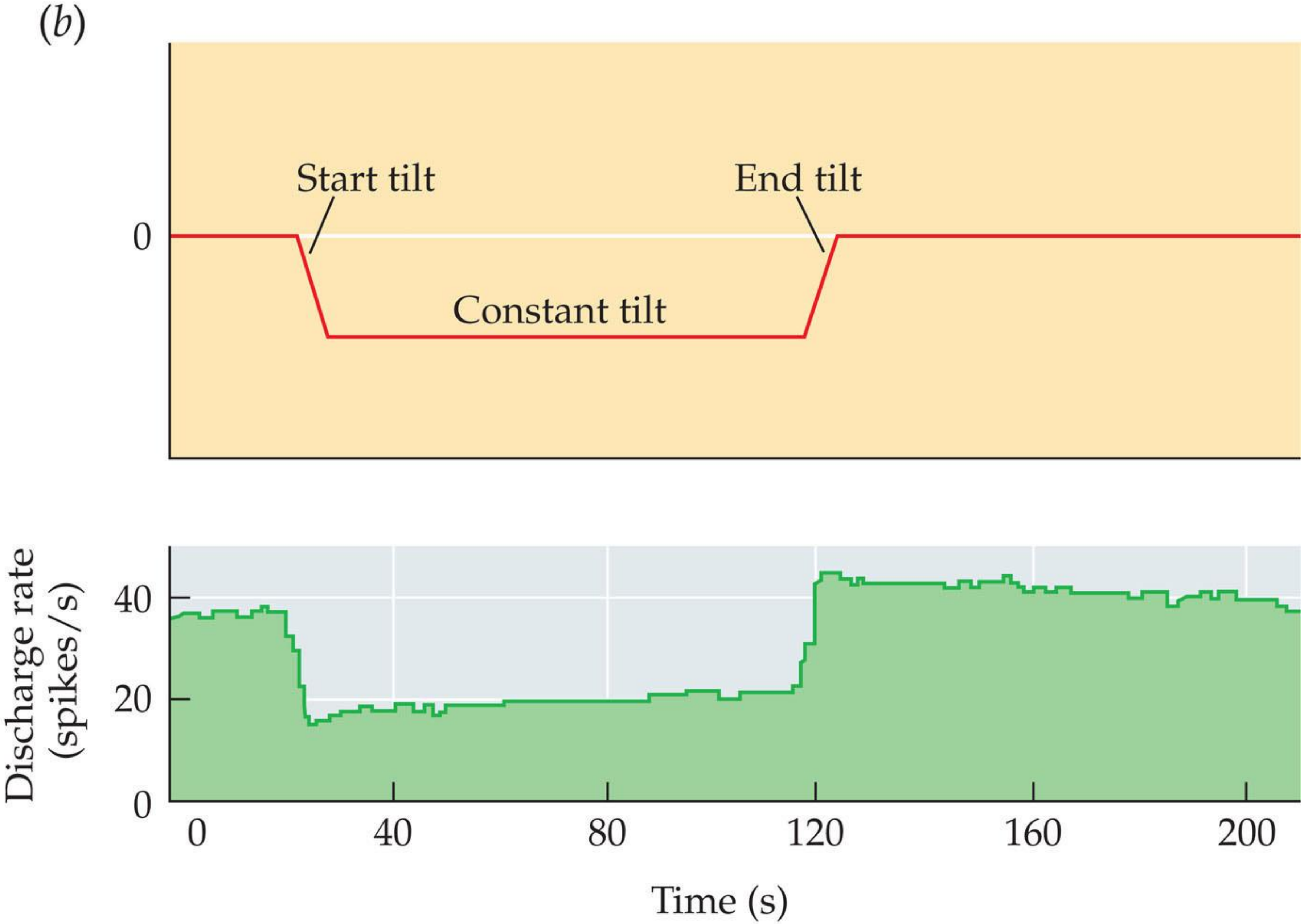
- Larger accelerations (or larger gravitational shear forces) move the otolith organ's otoconia more.
- This leads to greater deflection of the hair cell bundles.
- Change in receptor potential is proportional to magnitude of linear acceleration or gravitational shear.

Figure 12.15 Activity of a vestibular neuron innervating the utricle (Part 1)



SENSATION & PERCEPTION 4e, Figure 12.15 (Part 1)

Figure 12.15 Activity of a vestibular neuron innervating the utricle (Part 2)



SENSATION & PERCEPTION 4e, Figure 12.15 (Part 2)

Coding of direction in the otolith organs

- Arises in part from the anatomical orientation of the organs
- Utricular macula: horizontal plane
  - Sensitive to horizontal linear acceleration and gravity
  - Saccular macula: vertical plane
    - Sensitive to vertical linear acceleration and gravity

Spatial Orientation Perception

Three experimental paradigms are typically used to investigate spatial orientation perception.

1. Threshold estimation: What is the minimum motion needed to correctly perceive motion direction?
2. Magnitude estimation: Participants report how much (e.g., how many degrees) they think they tilted, rotated, or translated.
3. Matching: Participants are tilted and then orient a line with the direction of gravity. This is done in a dark room with only the line visible to avoid any visual cues to orientation.

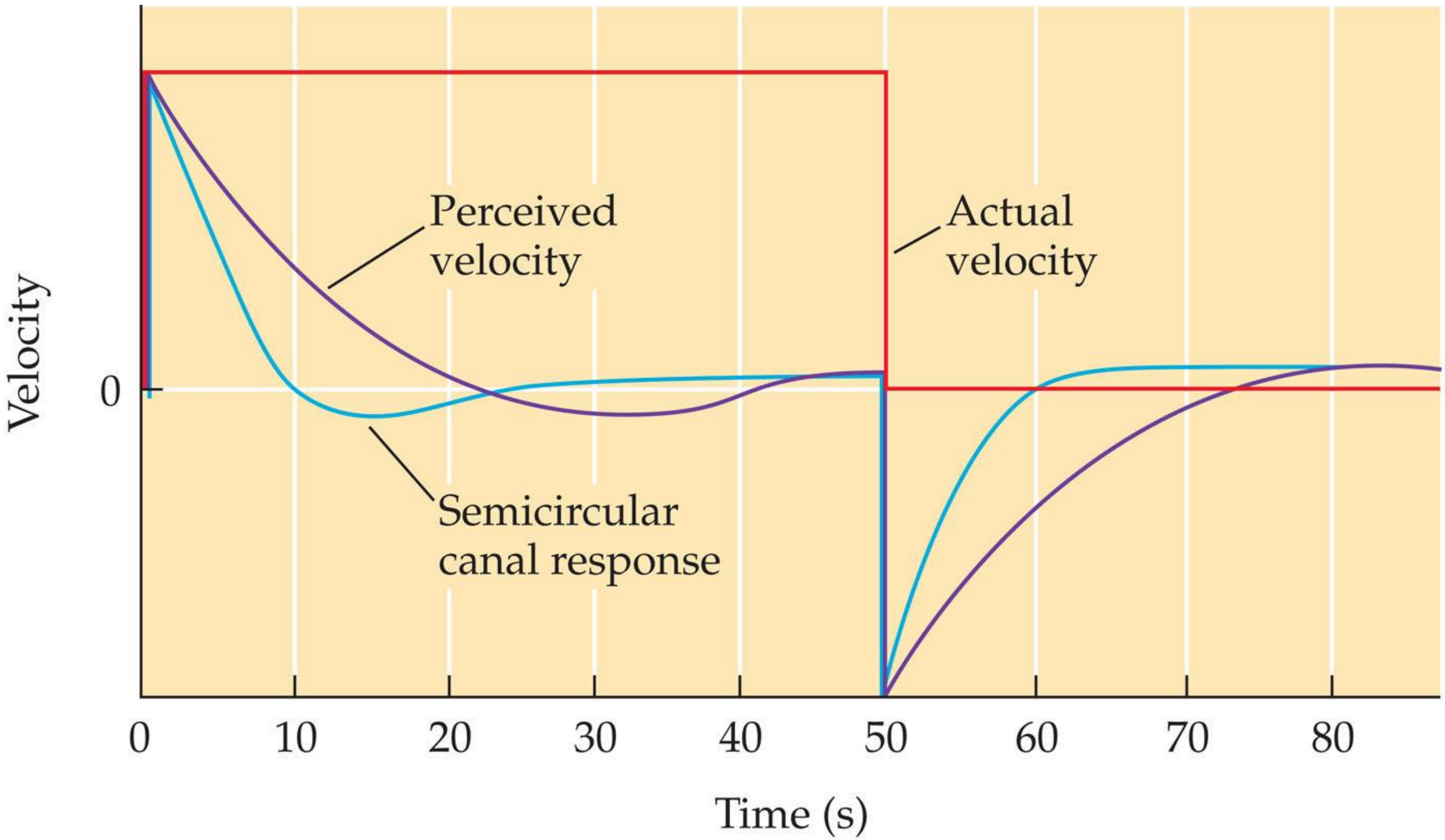
Rotation perception

- At first, constant rotation (in the dark) is perceived accurately.
- Soon, however, subjects feel as if they are slowing down.

Rotation perception (*continued*)

- After 30 s, they no longer feel as if they are rotating.
  - Time course of habituation for perceived velocity is slower than time course of habituation for velocity neurons: "Velocity storage"
- When rotation stops, subjects feel as if they are rotating in the *opposite* direction.

Figure 12.16 The red line shows the angular velocity of a person at rest, eyes closed, suddenly rotated at a constant speed for 50 seconds and then abruptly returned to rest

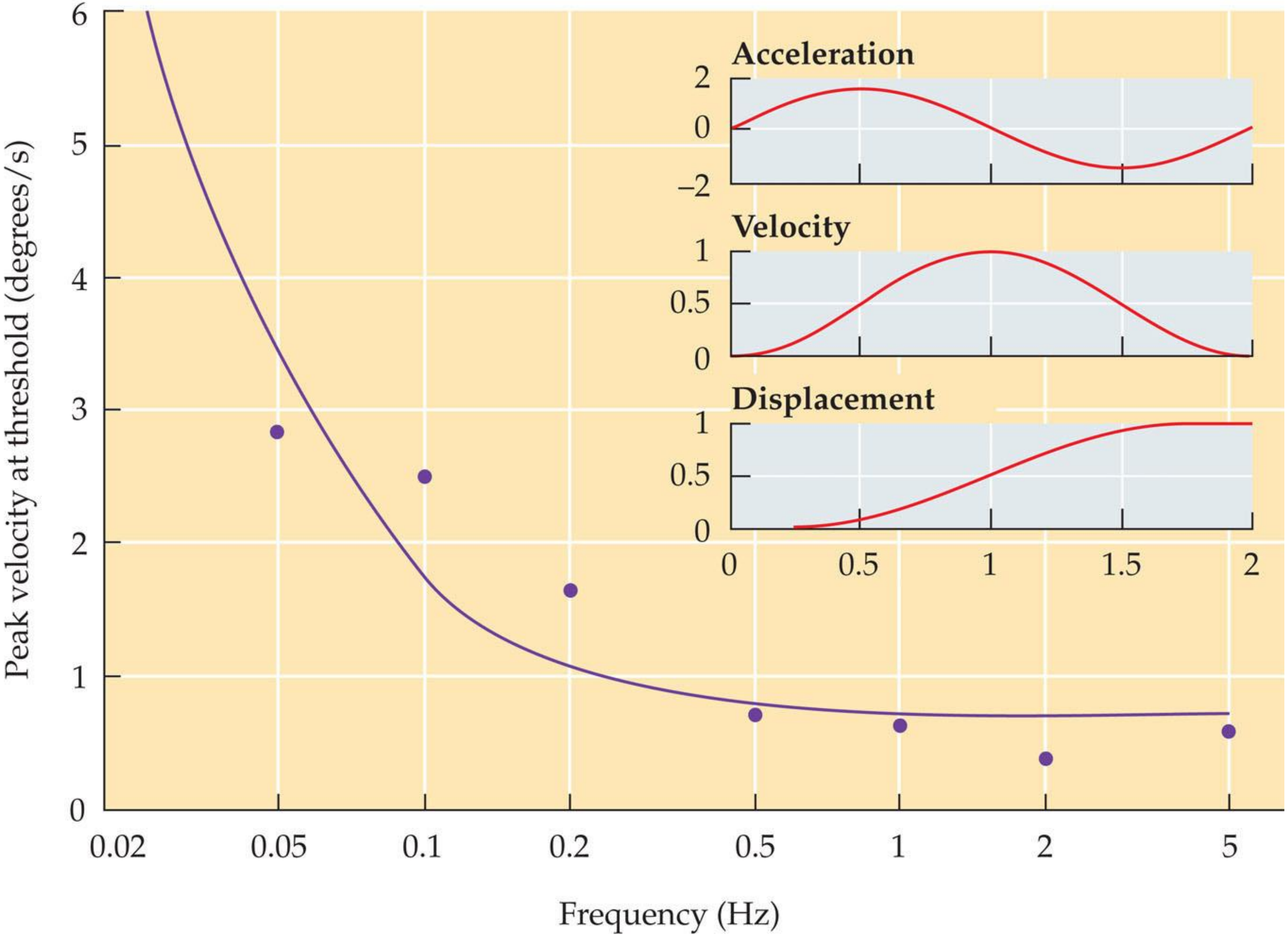


SENSATION & PERCEPTION 4e, Figure 12.16

Yaw rotation thresholds

- Humans are so sensitive to yaw rotation that we can detect movements of less than 1 degree per second
  - At this rate, it would take 6 minutes to turn completely around.
- As yaw rotation frequency decreases, it takes faster movement to be detected.

Figure 12.17 Mean velocity threshold as a function of frequency for seven subjects



SENSATION & PERCEPTION 4e, **Figure 12.17**

Translation perception

- When people are passively translated in the dark, they are able to use a joystick to reproduce the distance they traveled quite accurately.
- Interestingly, they also reproduce the velocity of the passive-motion trajectory.

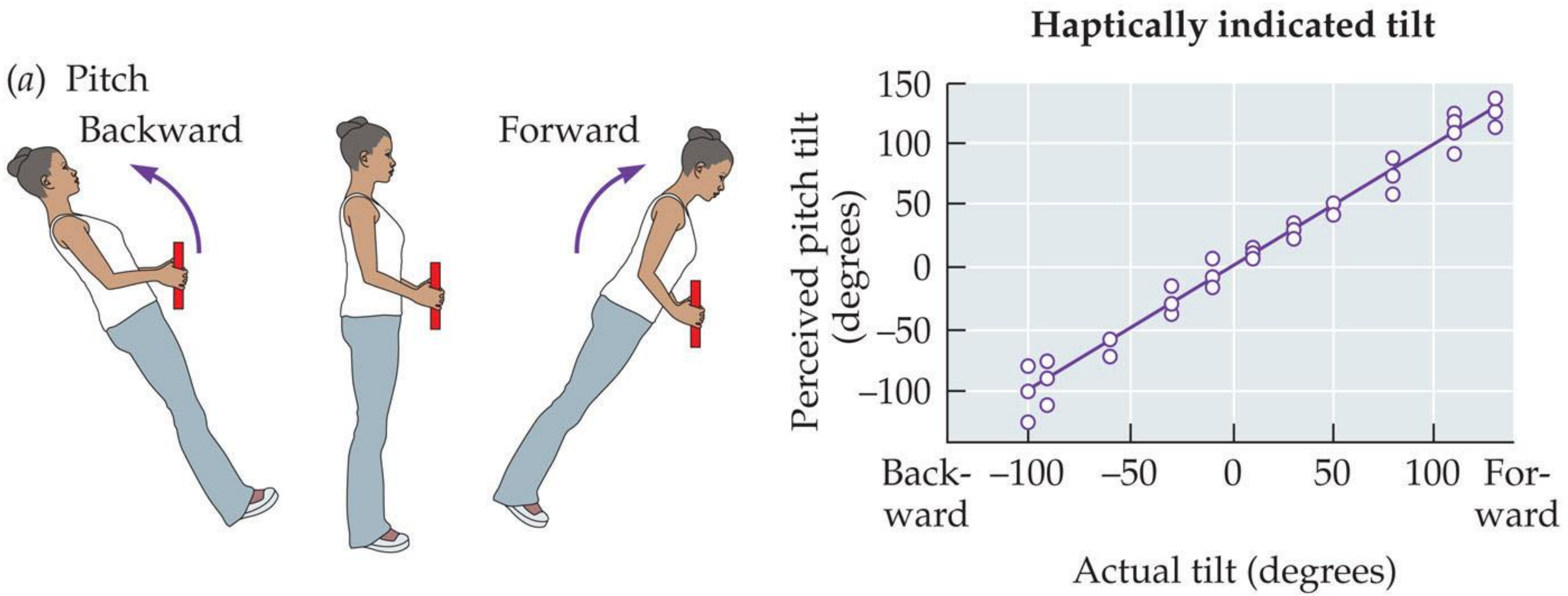
Translation perception (*continued*)

- This implies that the brain remembers and replicates the velocity trajectory.
  - The otolith organs register acceleration, and our brains mathematically integrate the acceleration and turn it into the perception of linear velocity.

Tilt perception

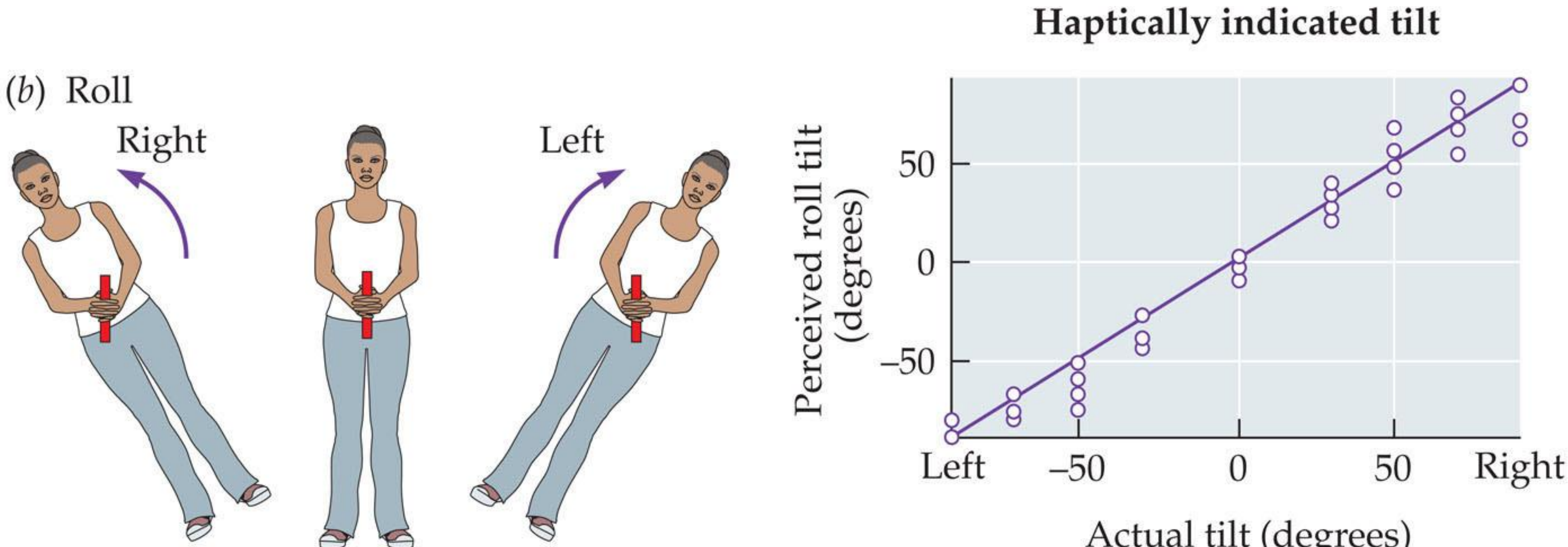
- We are very accurate when perceiving tilt for angles between 0 degrees (upright) and 90 degrees (lying down).
- Illusion: If you roll tilt your head to the left or right while looking at a vertical streak of light, the light appears to tilt in the opposite direction.

Figure 12.18 Subjects are generally pretty good at indicating how much they are tilted (Part 1)



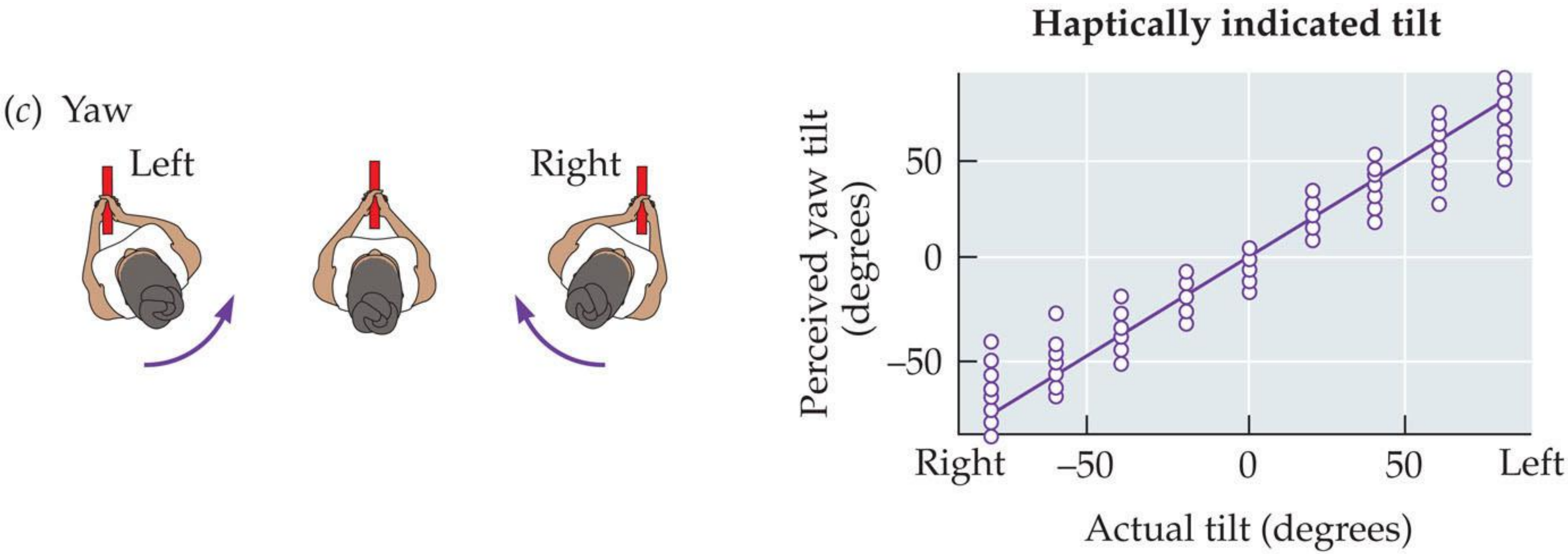
SENSATION & PERCEPTION 4e, Figure 12.18 (Part 1)

Figure 12.18 Subjects are generally pretty good at indicating how much they are tilted (Part 2)



SENSATION & PERCEPTION 4e, Figure 12.18 (Part 2)

Figure 12.18 Subjects are generally pretty good at indicating how much they are tilted (Part 3)



SENSATION & PERCEPTION 4e, **Figure 12.18 (Part 3)**

Sensory Integration

Sensory integration: The process of combining different sensory signals.

- Typically leads to more accurate information than can be obtained from individual senses alone

Visual-vestibular integration

- Vection: An illusory sense of self motion produced when you are not, in fact, moving.
  - Example: The feeling of flying while watching an IMAX movie
  - Example: Being stopped in your car at a light next to a semi. The semi begins to roll forward and you press on the brake because you feel as if you are rolling backwards.

Sensory Integration

Observers looking at a rotating display report rotational vection.

Subjects have the illusion of tilt but do not feel as if they turn upside-down.

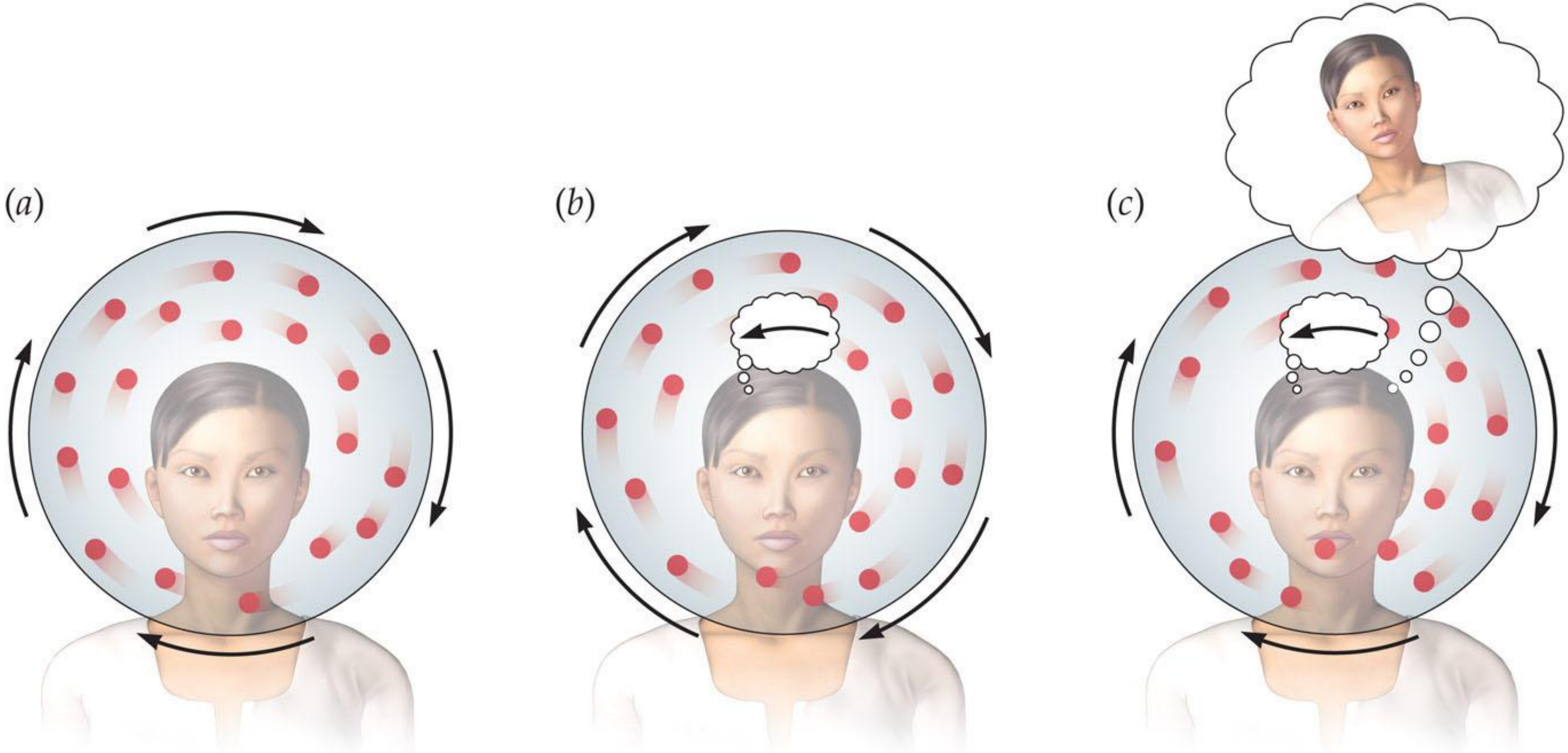
Sensory Integration

Why don’t people feel as if they are turning upside down?

- The vestibular system’s sense of gravity stops the illusion.
- Astronauts without gravity feel as if they are tumbling under these circumstances.

Thus, vestibular information is combined with visual information to yield a “consensus” about our sense of spatial orientation.

Figure 12.19 Rotational vection



SENSATION & PERCEPTION 4e, Figure 12.19

Active Sensing

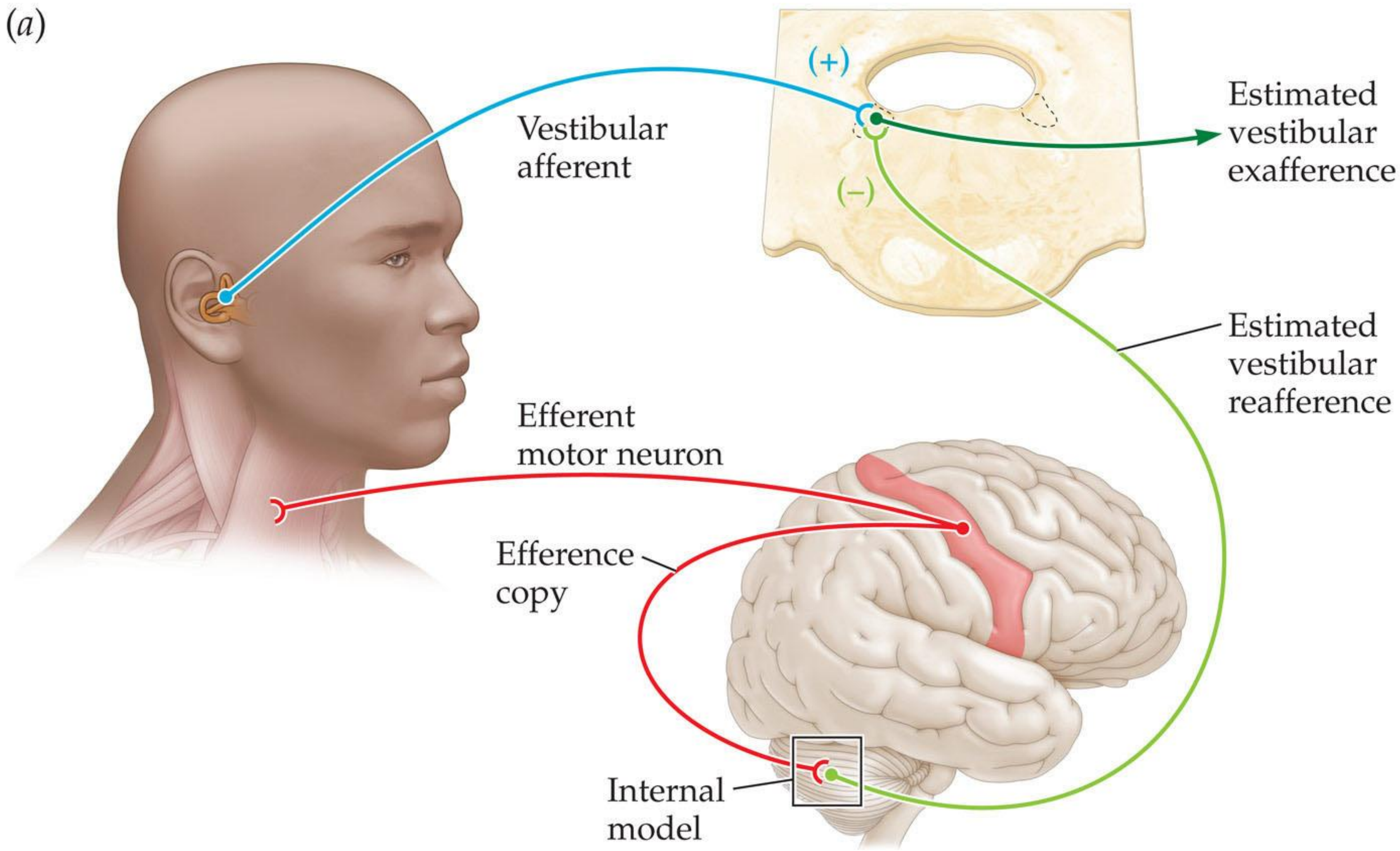
Our sensory systems must simultaneously integrate changes in sensation due to our own actions and changes in the external world.

- Sensory reafference: Change in afference caused by self-generated activity. For example, knowing that changes in visual stimulation are occurring because we are moving our head.

Active Sensing

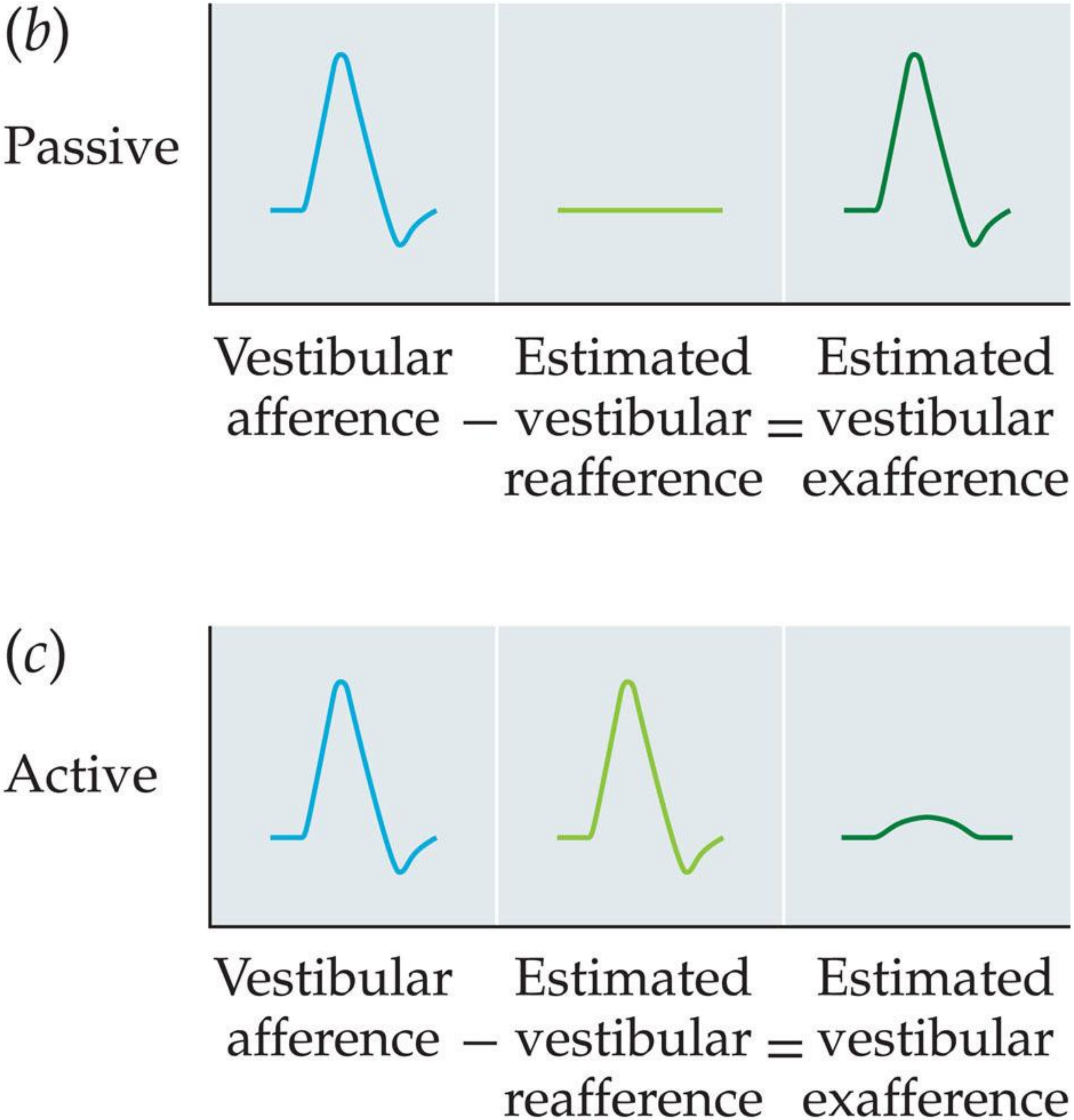
- Sensory exafference: Change in afference caused by external stimuli.
  - For example, knowing that changes in vestibular sensation are due to passive motion rather than self-generated motion

Figure 12.20 Simplified representation of the active vestibular sensing network (Part 1)



SENSATION & PERCEPTION 4e, Figure 12.20 (Part 1)

Figure 12.20 Simplified representation of the active vestibular sensing network (Part 2)



SENSATION & PERCEPTION 4e, **Figure 12.20 (Part 2)**

Reflexive Vestibular Responses

Balance system: The sensory systems, neural processes, and muscles that contribute to postural control.

- Includes the vestibular organs, kinesthesis, vestibulo-spinal pathways, skeletal bones, and postural control muscles

Reflexive Vestibular Responses

The balance system is more than just the vestibular system.

The vestibular system contributes more than just balance.

- Example: Vestibulo-autonomic reflexes help regulate blood pressure when lying down or standing up to maintain adequate blood flow to the brain.

Reflexive Vestibular Responses

Vestibulo-ocular reflexes (VORs): Counter-rotating the eyes to counteract head movements and maintain fixation on a target.

Angular VOR: The most well-studied VOR

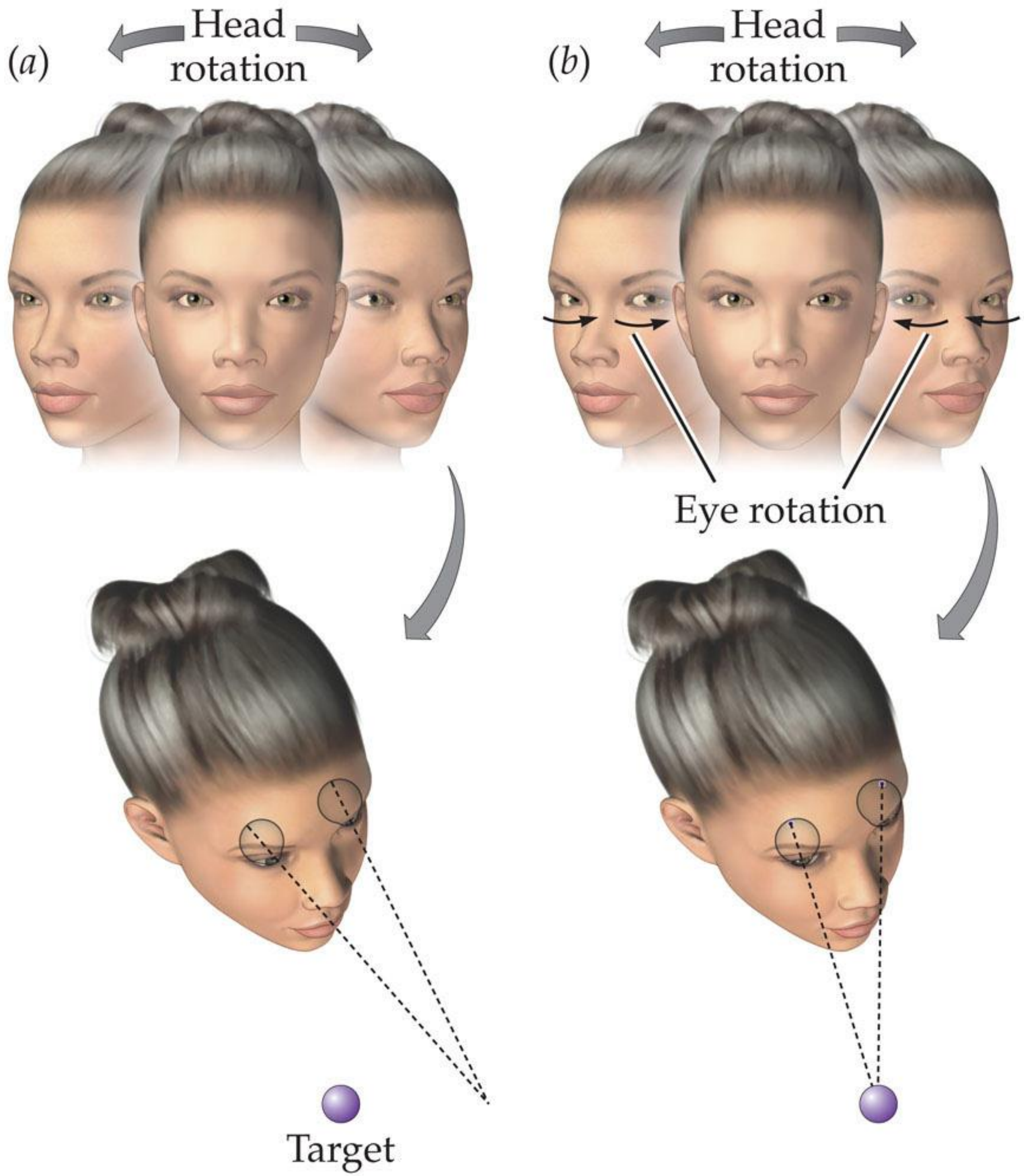
- Example: When the head turns to the left, the eyeballs are rotated to the right to partially counteract this motion.

Reflexive Vestibular Responses

Torsional eye movements: When the head is rolled about the x-axis, the eyeballs can be rotated a few degrees in the opposite direction to compensate.

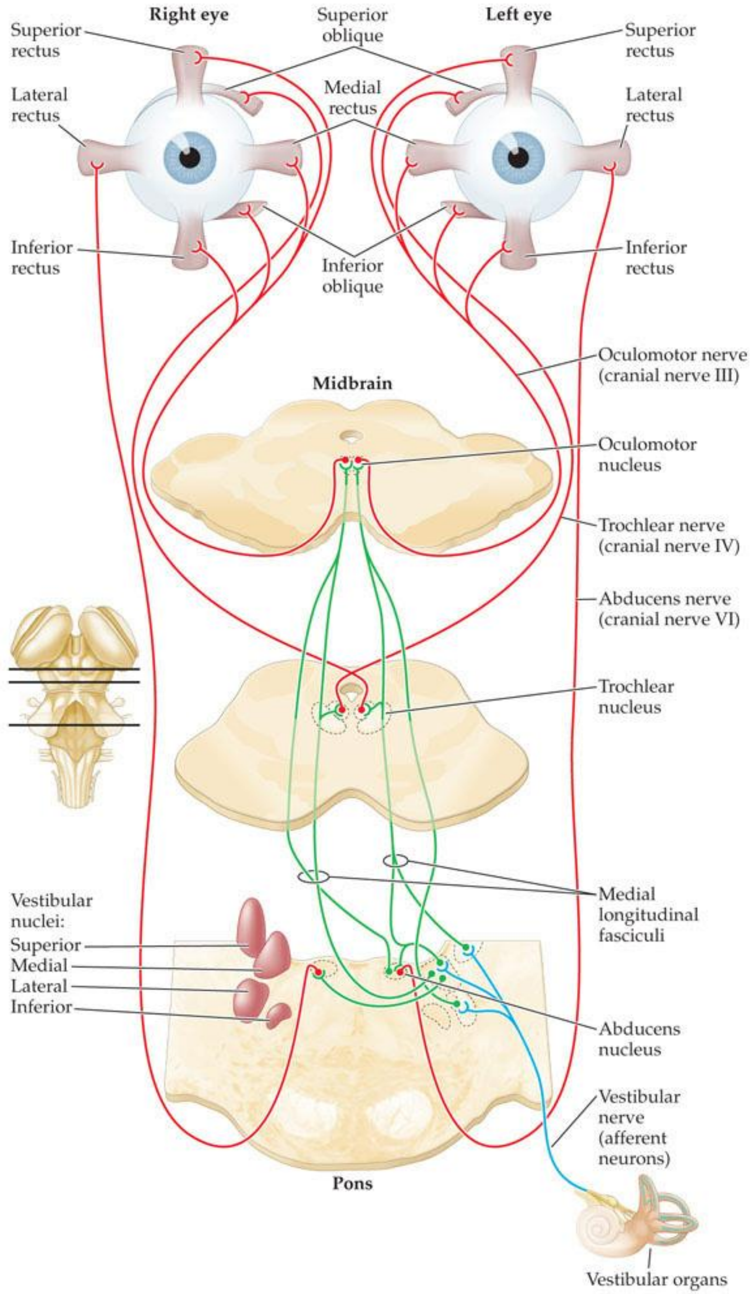
VORs are accomplished by six oculomotor muscles that rotate the eyeball.

Figure 12.21 Contribution of the angular VOR to visual stability



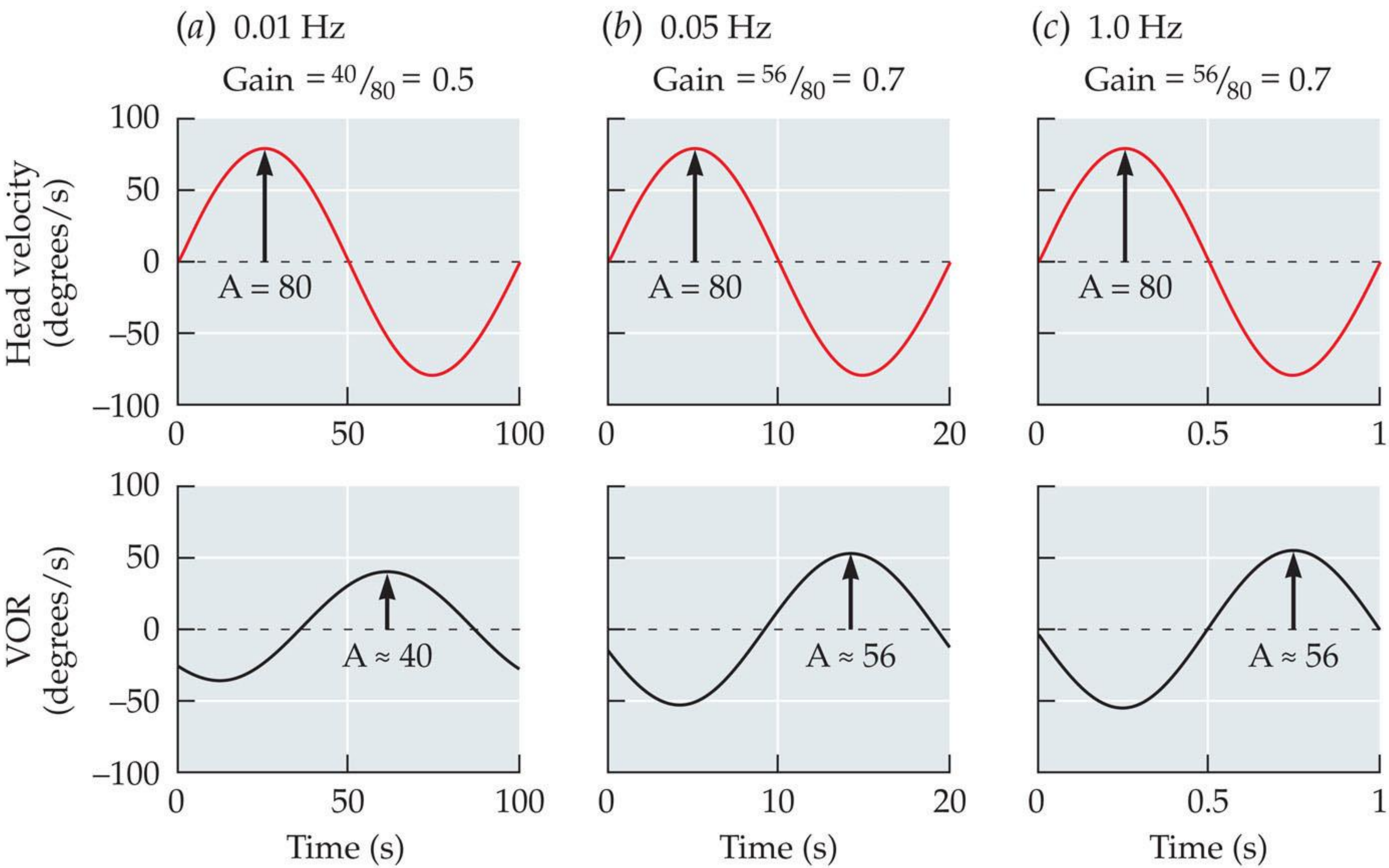
SENSATION & PERCEPTION 4e, Figure 12.21

Figure 12.22 Neural pathways for the three-neuron arc of the angular VOR



***SENSATION & PERCEPTION 4e*, Figure 12.22**

Figure 12.23 VOR responses in the dark at three frequencies



SENSATION & PERCEPTION 4e, Figure 12.23

Reflexive Vestibular Responses

Vestibulo-autonomic responses

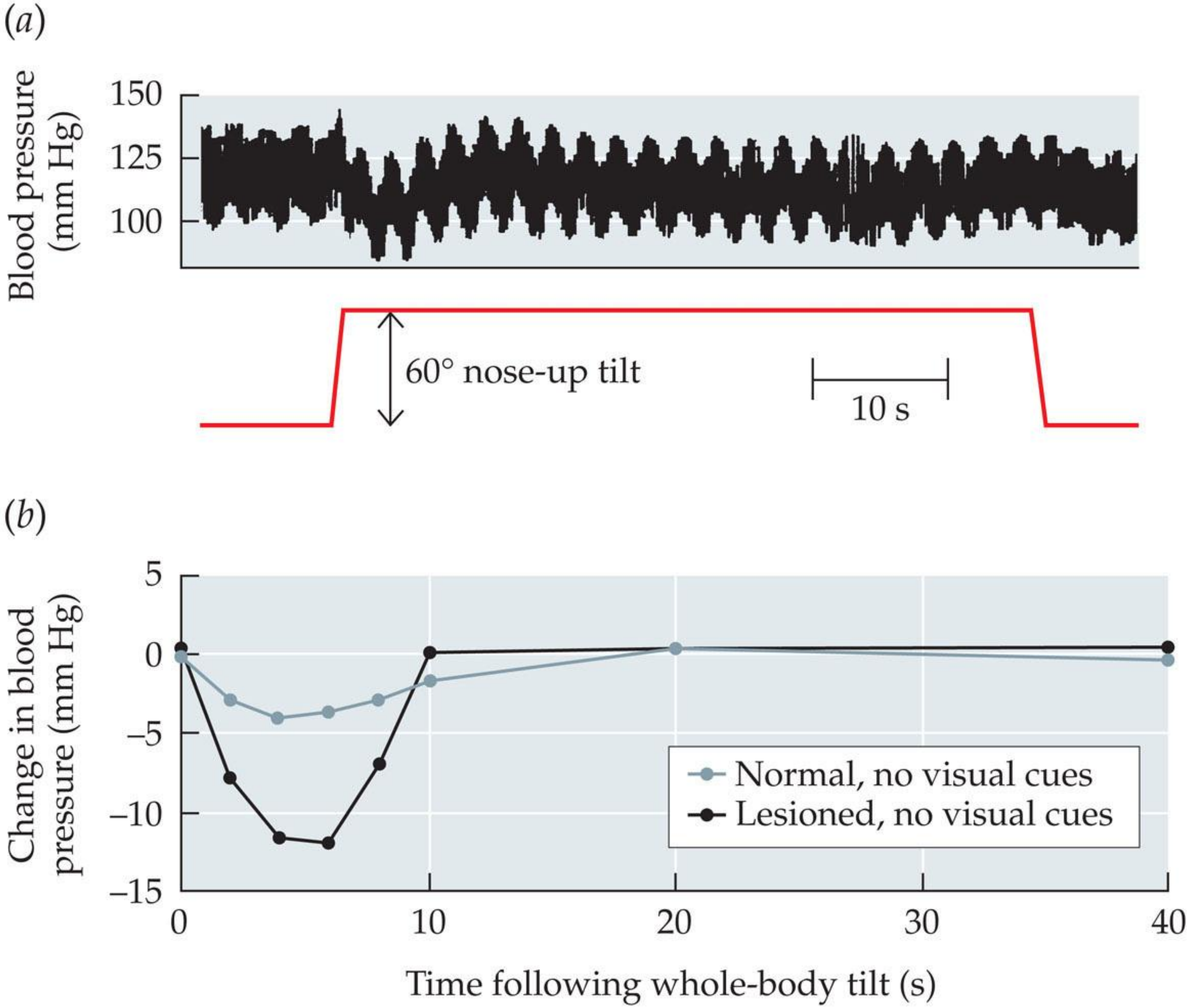
- Autonomic nervous system: The part of the nervous system that innervates glands, heart, digestive system, etc., and is responsible for regulating many involuntary actions.

Reflexive Vestibular Responses

Vestibulo-autonomic responses (*continued*)

- Motion sickness: Results when there is a disagreement between the motion and orientation signals provided by the semicircular canals, otolith organs, and vision.
  - Could be an evolutionary response to being poisoned
- Blood pressure is regulated by vestibulo-autonomic responses.

Figure 12.25 Vestibular influences on blood pressure



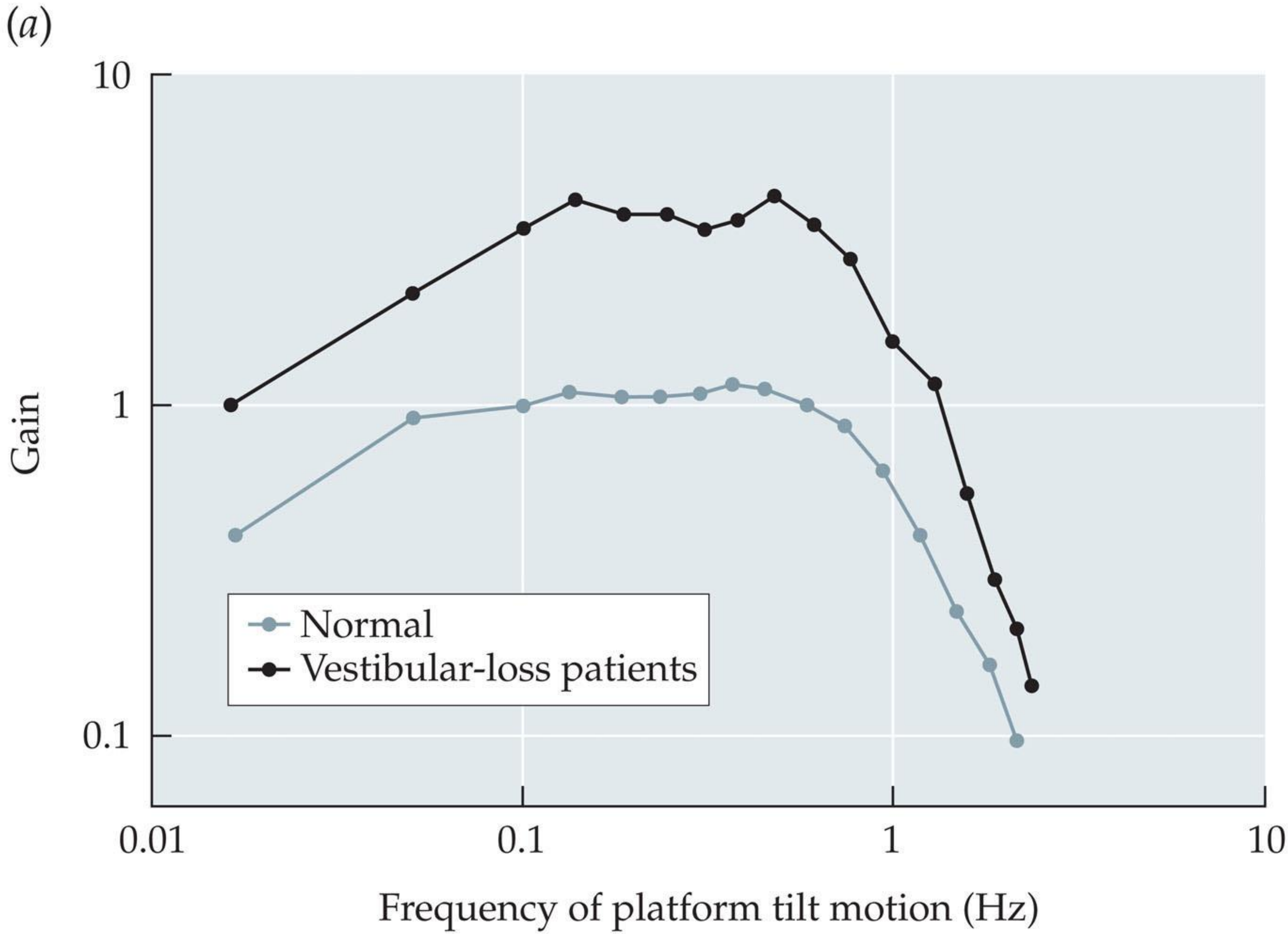
SENSATION & PERCEPTION 4e, Figure 12.25

Reflexive Vestibular Responses

Vestibulo-spinal responses

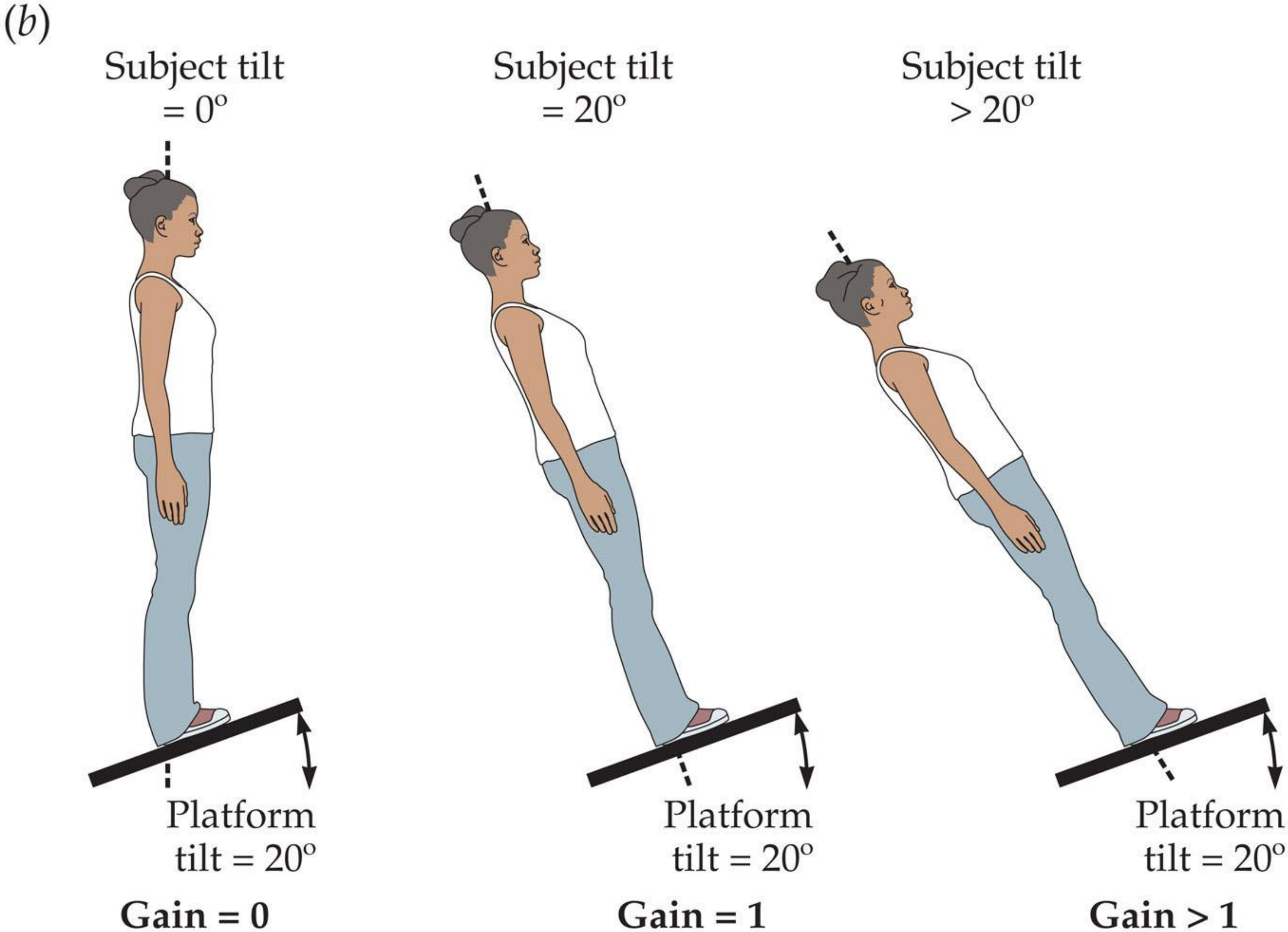
- A whole family of reflexes that work together to keep us from falling over
- Without vestibulo-spinal responses, we would be unable to stand up in the dark.
- Patients with vestibular loss actually over-compensate for body sway.

Figure 12.26 Demonstration of the contributions of the vestibular system to balance (Part 1)



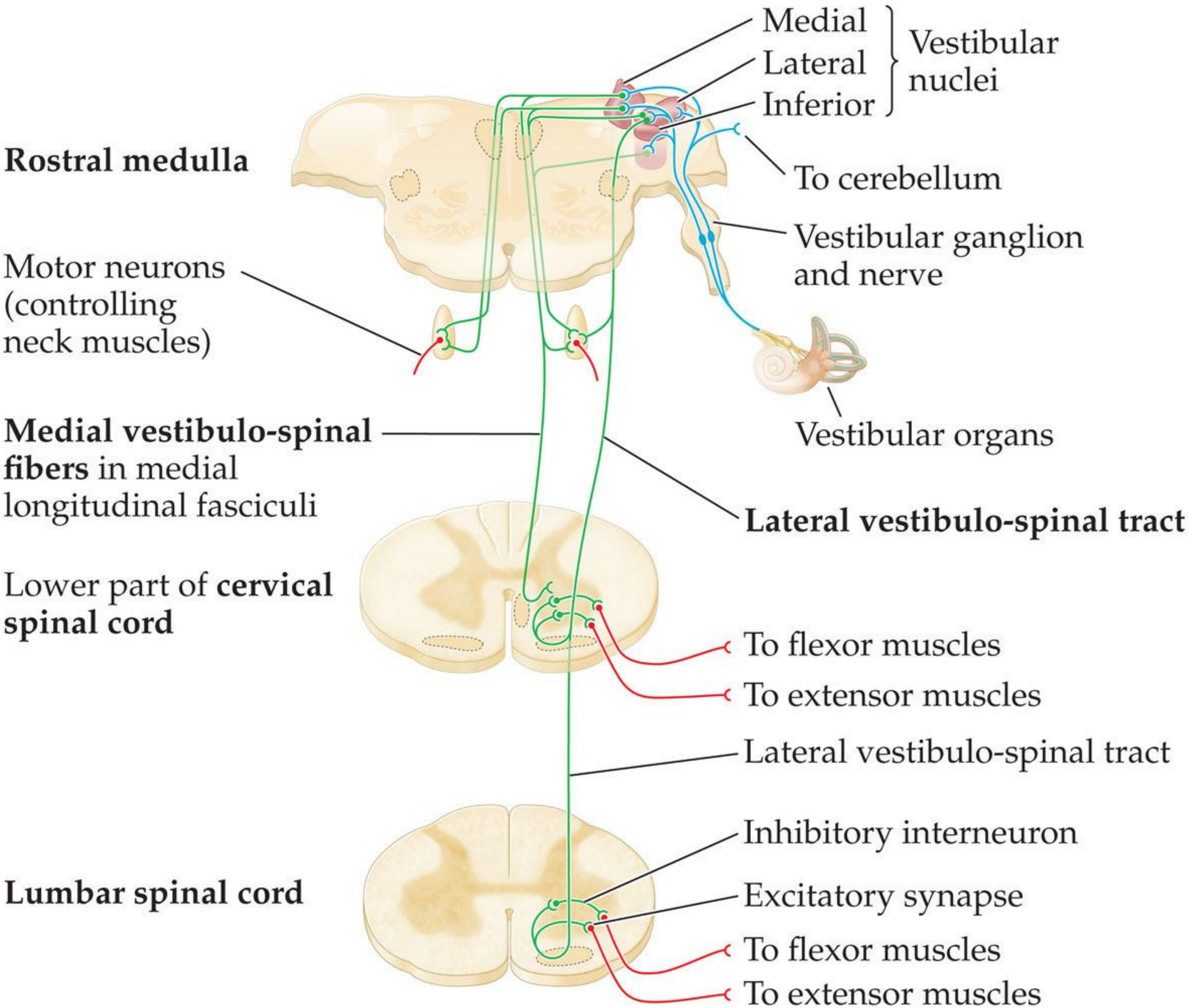
SENSATION & PERCEPTION 4e, Figure 12.26 (Part 1)

Figure 12.26 Demonstration of the contributions of the vestibular system to balance (Part 2)



SENSATION & PERCEPTION 4e, Figure 12.26 (Part 2)

Figure 12.27 Neural pathways for vestibulo-spinal reflexes



SENSATION & PERCEPTION 4e, Figure 12.27

Spatial Orientation Cortex

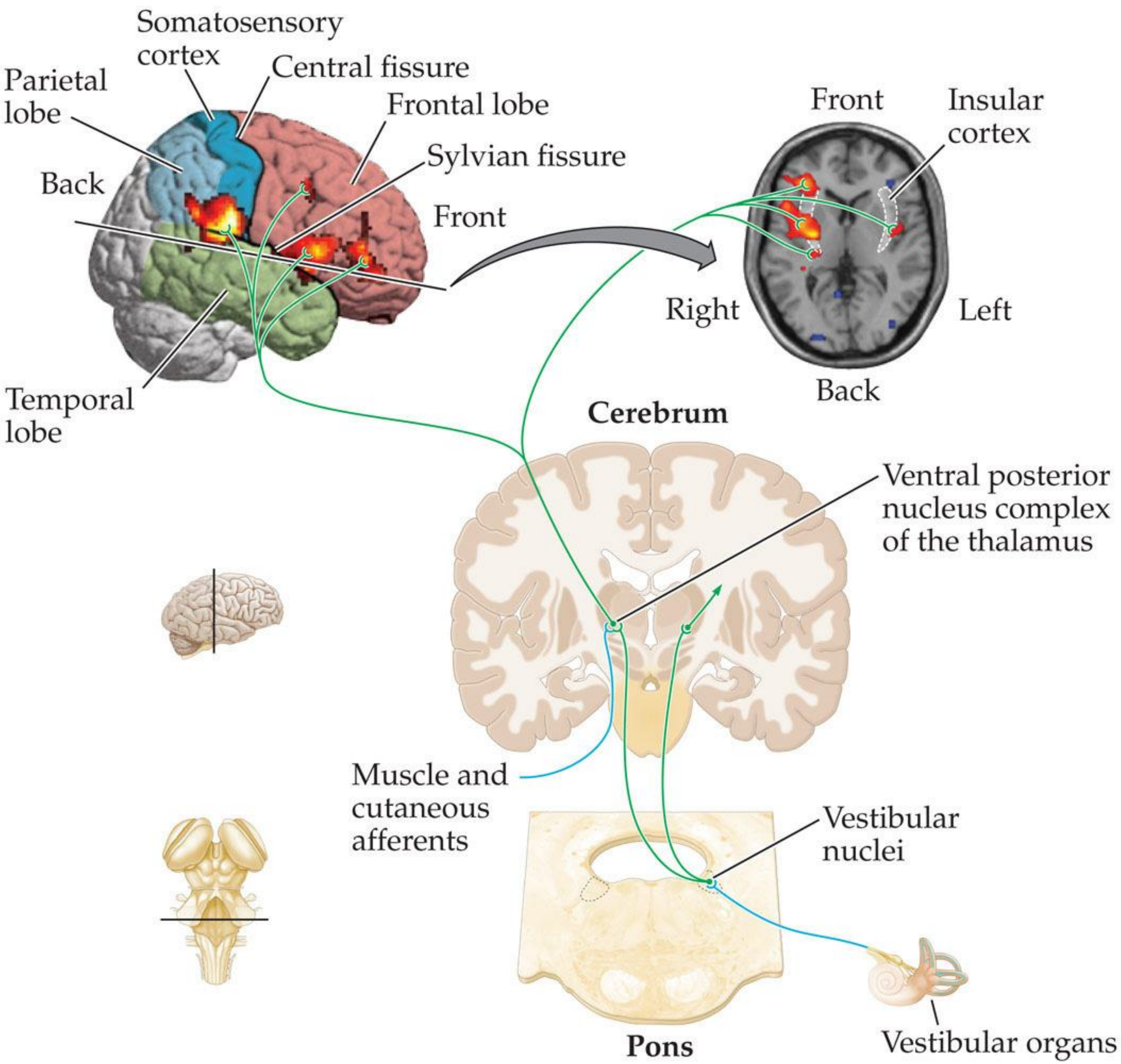
We have a visual cortex and an auditory cortex; do we have a vestibular cortex?

- Not really
- Areas of cortex respond to vestibular input, but they tend to respond to visual input as well.
  - No need to have cortex for processing vestibular information in isolation if visual information is available also.

Spatial Orientation Cortex

- Vestibular information reaches the cortex via thalamo-cortical pathways.
- Areas of cortex that receive projections from the vestibular system also project back to the vestibular nuclei.
  - Knowledge and expectations can influence perception of tilt and motion.

Figure 12.28 Ascending vestibular pathways pass from the vestibular nuclei to the thalamus on their way to the cortex



SENSATION & PERCEPTION 4e, Figure 12.28

When the Vestibular System Goes Bad

Since the vestibular system has such a widespread influence, what happens when it fails?

Possible problems:

- Spatial disorientation
- Imbalance
- Distorted vision unless head is held perfectly still
- Motion sickness
- Cognitive problems

When the Vestibular System Goes Bad

Mal de debarquement syndrome

- Swaying, rocking, or tilting perceptions felt after spending time on a boat or in the ocean
- Aftereffect of adapting to the rocking motion of the ocean
  - “Getting your sea legs”
- Usually goes away after a few hours, but some people experience it continuously, causing problems

Ménière's syndrome

- Sudden experience of dizziness, imbalance, and spatial disorientation
  - Can cause sudden falling down
  - Can cause repeated vomiting from severe motion sickness
- The unpredictability of the attacks can be terrifying for those who suffer from it.
- Possible treatments: medications, implanted devices, or sometimes removal of the vestibular apparatus itself!

Sensation & Perception in Everyday Life: Amusement Park Rides—Vestibular Physics Fun

Amusement park rides

- Much of what is enjoyable about roller coasters are the vestibular sensations.
- Twists and turns on a roller coaster are there primarily to yield vestibular sensation.
- Combination of high angular velocities sensed by the semicircular canals and rapid linear accelerations sensed by the otolith organs