CHAPTER 55: SENSORY SYSTEMS

CHAPTER SYNOPSIS

Sensory information reaches the central nervous system through the processes of stimulation, transduction, transmission, and interpretation. The three classes of environmental stimuli use different classes of receptors. Exteroceptors sense external, environmental conditions that affect the body, while interoceptors sense internal conditions of the body. The external environment is sensed at many levels. The least encompassing determines only that an object is present. Another level senses information indicating both the location and direction of an object, thereby providing a three-dimensional image of the object and its surroundings. In general, sensory receptors initiate nerve impulses by opening stimulus-gated ion channels that cause depolarization.

The simplest receptors are bare nerve endings that depolarize in response to direct physical stimulation. Such receptors sense changes in temperature by detecting heat and cold. Simple mechanical receptors include nociceptors that sense pain, spindle fibers that fire when a muscle is stretched, and baroreceptors that alter their rate of firing with changes in blood pressure. The Meissner's corpuscles and Merkel cells involved in two aspects of the sense of touch are simple mechanoreceptors as are Pacinian corpuscles that respond to changes in pressure and thereby sense vibration. Mechanoreceptors also sense changes in mechanical force thereby detecting changes in muscle length and tension through muscle spindles and blood pressure through baroreceptors in certain blood vessels.

Some sensory cell membranes contain special proteins that bind to certain chemicals in the environment or a cell's extracellular fluid The simplest receptors are chemical in nature and sense what we call taste and smell. Sensing the chemical environment is accomplished by taste receptors all over a fish's body and by smell receptors in the nasal cavity of terrestrial vertebrates. Internal chemoreceptors also sense changes in blood chemistry by measuring concentrations of pH and oxygen. Fish possess receptors that sense changes in the patterns of pressure waves in water. This is the lateral line system located in grooves on either side of the body. Various receptors provide information on the body's position in space. Statocysts are gravity receptors located in hollow chambers within the inner ear of vertebrates. Angular acceleration in all planes is detected by the motion of fluid in three semicircular canals, also within the inner ear. Mechanical receptors within the ears of land animals sense pressure waves in air as the lateral line receptors sense pressure waves in water. Structures in the middle ear amplify the sound waves since they are weaker in air than in water. The auditory receptors are located within the cochlea of the inner ear. Sonar is an auditory sense that provides information analogous to vision as it allows for three-dimensional imaging.

The stimulus for vision is electromagnetic energy detected by the visual pigment *cis*-retinal within rod and cone cells in the eye. Although many groups of animals independently evolved eyes of some sort, all utilize the same pigment. The retina is composed of three layers of cells. Light passes through ganglion and bipolar cells before reaching the rods and cones closest to the external surface of the eyeball. The visual nerve impulse is unusual in that it is initiated by a hyperpolarization event. Predator eyes are located at the front of their head to increase stereoscopic vision; prey eyes are at the side to enlarge their field of view.

Vertebrates sense a variety of environmental stimuli in addition to sound and light waves. Pit vipers sense heat, a form of electromagnetic radiation of longer wavelengths than light. Extremely accurate stereoscopic imaging is possible due to the location of the receptors. Many aquatic organisms utilize electrical charges to send and receive information much as bats utilize sonar. Terrestrial animals have not evolved such sensory mechanisms because air is a very poor conductor of electricity. Recent studies indicate that great numbers of organisms, from bacteria to birds, are able to sense the earth's magnetic field. Little is known about the nature of magnetic receptors.

CHAPTER OBJECTIVES

- ä Describe how stimulation, transduction, transmission, and interpretation are necessary for neurosensory communication in the central nervous system.
- ä Differentiate between interoception and exteroception and indicate the simplest kind of receptor found in each.
- ä Briefly review how receptor potentials are formed as related to a generalized sensory receptor.
- ä Describe receptors that detect temperature, pain, touch and pressure, muscle length and tension, and blood pressure.
- ä Compare the senses of taste and smell in aquatic and terrestrial vertebrates.
- ä Describe the chemoreceptors that sense chemical characteristics of body fluids.
- ä Explain the purpose for and the operation of a fish's lateral line system.
- ä Compare the invertebrate and vertebrate sensors responsible for gravity and angular acceleration.
- ä Compare hearing in fishes and terrestrial vertebrates.
- ä Understand how the structures of the middle and inner ear result in the sense of hearing.
- ä Describe the nature of vision in terms of its stimulus, biochemistry, the structure of rod and cone cells, and the mechanical design of the vertebrate eye.
- ä Explain sensory transduction as it occurs in vertebrate photoreceptors.
- ä Understand how vision in prey animals differs from vision in their predators.
- ä Illustrate the unique sensory systems that have evolved in response to specific aquatic and terrestrial habitats.

KEY TERMS

baroreceptor	exteroceptor	Pacinian corpuscle
binocular vision	interoceptor	photoreceptor
chemoreceptor	mechanoreceptor	proprioceptor
color-blindness	nociceptor	receptor potential
cutaneous receptor	organ of Corti	thermoreceptor

CHAPTER OUTLINE

55.0 Introduction

I. INPUT TO CENTRAL NERVOUS SYSTEM VIA AFFERENT SENSORY NEURONS — fig 55.1

A. Arrive as Action Potentials

B. Project to Different Brain Regions, Associated with Different Sensory Modalities
1. Intensity of sensation based on frequency of impulses
2. Information based on identity of transmitting neurons and frequency

55.1 Animals employ a wide variety of sensory receptors

I. CATEGORIES OF SENSORY RECEPTORS AND THEIR ACTIONS

A. Path of Sensory Information to the CNS — fig 55.2
1. Stimulation: Physical stimulus on sensory receptor
2. Transduction: Stimulus produces electrochemical impulse on dendrites of sensory neuron
3. Transmission: Axon conducts action potential along afferent pathway to CNS
4. Interpretation: Brain creates sensory perception from events of afferent stimulation

B. Comparison of Sensory Receptors
1. Differ as to the nature of the stimulus that initiates this event
2. Three classes of environmental stimuli use different classes of receptors — tbl 55.1
   a. Mechanical forces: Mechanoreceptors
   b. Chemicals: Chemoreceptors
   c. Electromagnetic and thermal energy: Photoreceptors and others
3. Simplest sensory receptors are free nerve endings
   a. Respond to bending or stretching of sensory neuron membrane
   b. Respond to changes in temperature or chemicals in extracellular fluid
4. More complex receptors involve association with epithelial cells

C. Sensing the Exterior and Internal Environments
1. Exteroceptors sense the external environment
2. Information depends on receptor, medium in which stimulus travels
   a. Most sensory systems evolved in water, later adapted to air
   b. Many senses operate better in air than water, need no alteration
   c. Other senses required changes to work well in air: Hearing
   d. Few that work in water do not work in air: Electrical organs of fish
   e. Other senses evolved in the air that cannot work in the sea: Infrared vision
3. Sensory systems provide several levels of information
   a. Determine only that an object is present, call attention to object
   b. Location and direction of object, can move in relation to it
   c. Compose three-dimensional image of object and surroundings
4. Interoceptors sense stimuli that arise within the body
5. Receptors detect changes related to muscle length and tension, limb position, pain, blood chemistry, blood volume and pressure, body temperature
6. Internal receptors are generally simpler than exterior receptors
7. Comparison of interoceptors and exteroceptors — tbl 55.2

D. Sensory Transduction
1. Cells possess stimulus-gated ion channels in their membranes
   a. Application of stimulus opens or closes channels
   b. Resulting change in membrane permeability produces shift in membrane potential
2. Stimulus causes depolarization in sensory receptor — fig 55.3a
   a. Analogous to excitatory postsynaptic potential (EPSP) in postsynaptic cell
   b. Resulting depolarization of sensory cell called receptor potential
3. Receptor potential is graded, like EPSP
   a. Larger sensory stimulus produces greater degree of depolarization
   b. Decrease in size with distance from source
      1) Called decrement
      2) Small irrelevant stimuli do not reach cell body
   c. Action potentials initiated if depolarization reaches threshold
   d. Conducted to CNS by sensory axon — fig 55.3b

4. Greater stimulus, greater depolarization, higher frequency of action potentials
    a. Logarithmic relationship between stimulus intensity and action potential frequency
    b. Brain can interpret signal as indicating certain strength of sensory stimulus

55.2 Mechanical and chemical receptors sense the body's condition

I. DETECTING TEMPERATURE AND PRESSURE

A. Receptors on the Skin
1. Cutaneous receptors are formally classed as interoceptors
    a. Respond at border between external and internal environments
    b. Good examples of receptor specialization in structure and function
    c. Respond to heat, cold, pain, touch, and pressure
2. Skin contains two populations of thermoreceptors
    a. Naked endings of dendrites sensitive to temperature changes
        1) Cold receptors stimulated by lowering temperature, inhibited by warming
        2) Heat receptors stimulated by increasing temperature, inhibited by cooling
    b. Cold receptors found immediately below surface, warm receptors slightly deeper
    c. Thermoreceptors in hypothalamus
        1) Monitor temperature of blood
        2) Provide information about body's internal, core temperature

B. Pain Receptors
1. Stimulus that causes tissue damage is sensed as pain
2. Receptors called nociceptors
    a. Mostly free nerve endings throughout body, especially near surface
    b. May respond to various stimuli
        1) Extremes in temperature
        2) Intense mechanical stimulation
        3) Chemicals in extracellular fluid, including ones released by injured cells
    c. Receptor thresholds vary
        1) Some respond only to actual tissue damage
        2) Others respond before damage has occurred

C. Touch and Pressure
1. Mechanoreceptors in epidermis, dermis, and subcutaneous tissue fig 55.4
2. Fine touch receptors located on fingertips and face
    a. Precisely localize cutaneous stimuli
    b. Phasic receptors
        1) Intermittently activated
        2) Hair follicle receptors, Meissner's corpuscles on hairless body surfaces
    c. Tonic receptors
        1) Ruffini endings, touch dome endings (Merkel cells) on surface of skin
        2) Continuously activated
3. Receptors measure duration of touch and extent to which it is applied
4. Pacinian corpuscles are deep phasic pressure-sensitive receptors
    a. Located in subcutaneous tissue
    b. End of afferent axon surrounded by capsule of layers of cells and extracellular fluid
    c. Elastic capsule absorbs sustained pressure, axon ceases to produce impulses
    d. Monitor onset and removal of pressure, as in vibration

II. SENSING MUSCLE CONTRACTION AND BLOOD PRESSURE

A. Mechanoreceptors Sense Changes in Mechanical Force on Membrane
   1. Ion channels open in response to mechanical distortion of membrane
   2. Initiate depolarization, receptor potential
   3. Sensory nerve generates action potentials

B. Muscle Length and Tension
   1. Special muscle spindles are buried in muscles, parallel with fibers — fig 55.5
      a. Stretch-sensitive axon of sensory neuron wrapped around each spindle
      b. Spindle functions as stretch receptor, a type of proprioceptor
         1) Provide information about position or movement
         2) Conduct action potential to spinal cord
         3) Synapse with somatic motor neuron innervating muscles
   2. Muscle spindle elongates when muscle is stretched
      a. Cause motor neurons to produce action potentials, cause muscle to contract
      b. Pathway is basis for muscle stretch reflex including knee-jerk reflex
   3. Golgi tendon organs monitor tension at tendon-muscle boundary as muscle contracts
      a. If tension too great, elicit reflex to inhibit motor neurons to muscle
      b. Ensures that muscles do not contract too strongly, damaging their tendons

C. Blood Pressure
   1. Receptors in carotid sinus (in wall of carotid arteries) and in aortic arch
      a. Baroreceptors are highly branched networks of afferent neurons
      b. Detect tension in blood artery walls
   2. Rate of firing decreases with decrease in blood pressure
      a. CNS responds by stimulating sympathetic division of autonomic system
      b. Increases heart rate and vasoconstriction
      c. Raised blood pressure, maintains homeostasis
   3. Rate of firing increases with increase in blood pressure
      a. Reduces sympathetic activity, increases parasympathetic activity
      b. Slows heart, lowers blood pressure

III. SENSING TASTE, SMELL, AND BODY POSITION

A. Chemoreceptors Are Sensory Cell Membranes that Contain Special Proteins
   1. Bind to specific chemicals in environment or extracellular fluid
   2. With binding, membrane depolarizes, produces action potentials
   3. Involved in taste, smell, maintaining composition of blood and cerebrospinal fluid

B. Taste
   1. Mediated by taste buds, collection of chemosensitive receptors
      a. In fish, taste buds are located all over body, used to locate food
      b. Most sensitive vertebrate chemoreceptors
   2. In terrestrial vertebrates, taste buds concentrated on papillae in mouth — fig 55.6
      a. Humans respond to salt, sweet, sour, and bitter tastes
         1) Salty associated with Na^+ ions
         2) Sour associated with H^+ ions
         3) Molecules that produce sweet and bitter tastes are varied in structure
      b. Taste buds that respond best to certain taste are localized
         1) Sweet at tip
         2) Sour at sides
         3) Bitter at back
         4) Salty over most of surface

- c. Perception of taste is a combination of impulses from these axons
  - 1) Taste augmented by sense of smell
  - 2) Eat onion with nose open or plugged
- 3. Arthropod taste receptors
  - a. Flies have sensory receptors located on feet
    - 1) Hairs contain different chemoreceptors to detect sugar, salts — fig 55.7
    - 2) Proboscis extends to feed if feet step on potential food

C. Smell
- 1. Also called olfaction
- 2. In terrestrial vertebrates, located in upper portion of nasal passage — fig 55.8
  - a. Receptors are bipolar neurons with terminal tassels of cilia
  - b. Dendrites extend into nasal mucosa, axons project to cerebral cortex
- 3. Sense of smell used like a fish's sense of taste
  - a. Sense chemical environment around itself
  - b. Specialized to detect airborne particles since surrounded by air not water
  - c. Particles must dissolve in extracellular fluid to activate olfactory response
  - d. Extremely acute sense in many mammals
- 4. Sense thousands of different smells
  - a. May be a thousand different genes to code for different smell receptor proteins
  - b. Particular set of olfactory neurons respond to a given odor
  - c. That set serves as an odor fingerprint for identification

D. Internal Chemoreceptors
- 1. Sense variety of chemical characteristics of body fluids
- 2. Peripheral chemoreceptors
  - a. Aortic and carotid bodies embedded within walls of certain arteries
  - b. Sensitive mostly to plasma pH
- 3. Central chemoreceptors
  - a. Found in medulla of brain
  - b. Sensitive to pH of cerebrospinal fluid (CSF)
- 4. Involved in controlling respiratory activity
  - a. With low breathing rate
    - 1) O_2 levels decrease producing carbonic acid
    - 2) pH decreases rapidly
    - 3) CO_2 enters CSF and reduces pH, stimulates central chemoreceptors
  - b. Indirectly affects brain stem respiration control center, increases breathing rate
  - c. Aortic sensitivity to O_2 only important at high altitudes

E. The Lateral Line System
- 1. Provide fish with sense of "distant touch"
  - a. Sense objects that reflect pressure waves, low-frequency vibrations
  - b. Allow fish to detect prey, swim synchronously with rest of school
  - c. Enables blind cave fish to sense environment, monitor changes in water flow
- 2. Found in amphibian larva, lost during metamorphosis, not found in land vertebrates
- 3. Supplements fish's sense of hearing (different sensory structure)
- 4. Composition of the lateral line system
  - a. Structures within longitudinal canal along body, several canals in head — fig 55.9a
  - b. Neurons called hair cells — fig 55.9b
    - 1) Hairlike processes project into gelatinous membrane called cupula
    - 2) Hair cells innervated by neurons that transmit impulses to brain
    - 3) Stereocilia are processes of same length
    - 4) Kinocilium is single, longer projection
- 5. How system functions

a. Vibrations in environment produce movement of cupula
b. Causes hair cells to bend
c. Stimulation of sensory neurons when stereocilia bend in direction of kinocilium
1) Generates receptor potential
2) Frequency of action potentials increased
d. Stereocilia bend in opposite direction, inhibit activity of sensory neuron

F. Gravity and Angular Acceleration
1. Invertebrate orientation
a. Statocysts help brain determine orientation of body with respect to gravity
b. Statocysts are ciliated hair cells
1) Cilia embedded in gelatinous membrane with calcium carbonate crystals
2) Crystals called statoliths
3) Increase mass of membrane so it can bend cilia when head position changes
4) Head tilts to right, membrane bends cilia on right side, activates neurons
2. Vertebrate receptors are in membranous labyrinth in inner ear
a. Labyrinth is system of fluid-filled chambers and tubes
1) Comprise organs of equilibrium and hearing
2) Surrounded by perilymph fluid and bone
3) Labyrinth fluid called endolymph
4) Entire structure is size of a pea
b. Receptors for gravity composed of saccule and utricle chambers fig 55.10
1) Chambers possess hair cells with stereocilia and kinocilium
2) Each contains gelatinous matrix containing calcium carbonate otoliths
3) Membrane is called otolith membrane
c. Otolith organ in each chamber oriented differently
1) Utricle more sensitive to horizontal acceleration (moving car)
2) Saccule sensitive to vertical acceleration (elevator)
3) Acceleration causes stereocilia to bend, produces action potentials in neuron
3. Angular acceleration sensed via three adjacent semicircular canals
a. Oriented in three different planes to detect motion in any direction
1) Canals are fluid-filled fig 55.11
2) Ends of canals are swollen ampullae chambers
3) Cilia of another group of hair cells protrude into ampulla
4) Tips of cilia embedded with wedge of gelatinous material, the cupula
5) Cupula protrudes into endolymph of each semicircular canal
b. Rotation of head causes movement of fluid, pushes against cupula
1) Deformation of cupula bends cilia
2) Bending of cilia depolarizes or hyperpolarizes hair cells
3) Similar to mechanism of fish lateral line system
4) Stereocilia bent in direction of kinocilium produces depolarization
4. Vestibular apparatus: Saccule, utricle, and semicircular canals
a. Saccule and utricle sense linear acceleration
b. Semicircular canals sense angular acceleration
c. Information from all help maintain body's position in space, balance, equilibrium

55.3 Auditory receptors detect pressure waves in the air

I. THE EARS AND HEARING

A. Aquatic Versus Terrestrial Sensations
1. Fish use lateral line system to detect pressure waves in water
2. Terrestrial vertebrates detect vibration in air via mechanical receptors in the ear
a. Analogous to and evolved from lateral line organs in fish

b. Sense more accurate in water than in air, water transmits waves more efficiently
3. Terrestrial vertebrates highly dependent on hearing
   a. Monitor environment
   b. Communicate with species members
   c. Detect sources of danger fig 55.12
4. Advantages of auditory stimuli
   a. Stimuli travel farther and faster than chemical stimuli
   b. Provides more information about direction than chemoreceptors
   c. Provide little information about distance

B. Structure of the Ear
1. Fish use lateral line system and hearing
   a. Detect water movements and vibrations from near objects via lateral line system
   b. Use hearing to detect vibrations from a greater distance
2. Structure of the fish hearing system
   a. Otolith organs in membranous labyrinth (utricle and saccule)
   b. Also includes outpouching of labyrinth called lagena
   c. Sound waves travel through watery body of fish as easily as through water
   d. Calcium carbonate otolith has different density to detect sound
   e. Some fish use air-filled swim bladder to serve same function
      1) Include catfish, minnows, suckers
      2) Chain of small bones, Weberian ossicles, transmit vibrations to saccule
3. Terrestrial vertebrates evolved ears for hearing fig 55.13
   a. Outer ear
      1) Vibrations channel through ear canal
      2) Directed onto ear drum, tympanic membrane
   b. Middle ear
      1) Three small bones move in response to vibrations on ear drum
      2) Malleus = hammer, incus = anvil, stapes = stirrup
      3) Middle ear bones analogous to Weberian ossicles in fish
      4) Eustachian tube connects middle ear to throat
         a) Equalizes pressure between middle ear and environment
         b) "Popping" of ears with rapid changes in altitude to equalize pressure
   c. Inner ear
      1) Stapes vibrates against oval window, membrane that leads to inner ear
      2) Oval window smaller than ear drum, vibrations produce more force per area
      3) Cochlea is coiled, fluid-filled chamber in inner ear
         a) Bony structure, contains part of labyrinth called cochlear duct
         b) Cochlear duct located in center of cochlea
         c) Vestibular canal lies above it
         d) Tympanic canal lies below it
         e) All three chambers are fluid-filled
         f) Oval window opens to upper vestibular canal
         g) Stapes pushes on oval window causes it to vibrate
         h) Vibrations set up pressure waves in fluid
         i) Pressure waves travel down to tympanic canal
         j) Waves push round window to transmit pressure back to middle ear

C. Transduction in the Cochlea
1. Pressure waves produced by oval window vibrations transmitted through cochlea
   a. Causes cochlear duct to vibrate
   b. Cause vibrations in basilar membrane, bottom surface of cochlear duct
2. Sensory hair cells located on surface of basilar membrane
   a. Similar to other hairlike organs, but lack kinocilium

b. Cilia project into overhanging gelatinous membrane called the tectorial membrane
c. Organ of Corti: Basilar and tectorial membranes plus hair cells
d. Basilar membrane vibration bends hair cell cilia as it moves relative to the tectorial membrane
e. Bending depolarizes the hair cells
f. Hair cells stimulate action potentials in sensory neurons going to brain
g. Impulses interpreted as sound

D. Frequency Localization in the Cochlea
1. Basilar membrane composed of elastic fibers of varying length and stiffness
a. Short and stiff at base of cochlea (near oval window) = high resonant frequency
b. Long and flexible at apex (far end) = low resonant frequency
c. Sound wave energy moves basilar membrane up and down
d. Energy imparted to region with most similar resonant frequency fig 55.14
e. Causes maximum deflection at that point
f. Depolarization of hair cells greatest at that point
g. Action potentials arriving in brain interpreted as sound of that frequency or pitch
2. Flexibility of basilar membrane limits human hearing
a. Frequency range of 20-20,000 cycles per second (Hz) in children
b. Hearing high-pitch sounds declines with age
c. Other vertebrates sense sounds lower than 20 Hz, higher than 20,000 Hz
3. Hair cells are innervated by efferent axons from brain
a. Impulses can make hair cells less sensitive
b. Increase individual's ability to concentrate on one signal
c. Other sounds effectively tuned-out by efferent axons

II. SONAR

A. Special Adaptation Possessed by Few Animals
1. Two ears of terrestrial vertebrates enable localization of sound
a. Can be used to determine direction
b. Not highly accurate to provide measure of distance
2. Sonar circumvents limitations of living in darkness
a. Bat can avoid a wire less than 1 millimeter in diameter fig 55.15
b. Examples: Shrew, whale, dolphin
3. Echolocation
a. Emit sounds, determine time for sound to reach object and return
b. Allows for three-dimensional imaging
4. Allows bats to occupy same environment as birds, but in darkness

55.4 Optic receptors detect light over a broad range of wavelengths

I. EVOLUTION OF THE EYE

A. Visual Stimulus Is Light Energy
1. Travels in straight line, arrives almost instantaneously
2. Provides information to determine direction and distance of objects
3. Invertebrates perceive light with eyespots, but cannot construct visual image
a. Pigment layer shading one side of eye enables detection of direction o f light
b. Flatworm eyespots have screening pigment on inner and back sides
1) Photoreceptor cells stimulated only by light from front fig 55.16
2) Flatworm swims in direction at which receptor cells are least stimulated

4. Image forming eyes evolved independently in four different groups
    a. Include annelids, mollusks, arthropods, and vertebrates
    b. Similar in structure, evolved independently — fig 55.17
    c. All use same light-capturing visual pigment

B. Structure of the Vertebrate Eye
1. Vertebrate eyes are lens-focused — fig 55.18
    a. White of eye is the sclera, tough connective tissue
    b. Light passes through transparent cornea
        1) Begins to focus it
        2) Light bends when it passes from medium of one density to another
    c. Iris is the colored portion of the eye
        1) Composed of muscles that change size of pupil opening
        2) Size of pupil decreases in bright light
        3) Light passes through transparent pupil
    d. Light continues through lens which completes focusing process
        1) Lens is a fat disk
        2) Attached by suspensory ligaments to ciliary muscles
    e. Shape of lens influenced by tension in suspensory ligament
        1) Contraction of ciliary muscles puts slack in suspensory ligament
            a) Lens becomes rounded, more powerful
            b) Process necessary for close vision
        2) Relaxation of ciliary muscles tightens suspensory ligament
        3) Lens becomes flatter, less powerful
        4) Keeps image focused on retina
    f. Nearsighted and farsighted: Improper focus of image on retina — fig 55.19
    g. Fish and amphibian lenses have a constant shape
        1) Focusing achieved by moving lens in and out
        2) Similar to focusing a camera

II. VERTEBRATE PHOTORECEPTORS

A. Retina Contains Rods and Cones — fig 55.20
1. Rods used for black-and-white vision when illumination is dim
2. Cones are used for color vision, are shorter than rods
    a. Humans have 100 million rods and 3 million cones in each retina
    b. Most cones found in fovea
        1) Location where eye forms its sharpest image
        2) Almost no rods found here
3. Cellular structure of rods and cones very similar
    a. Inner segment
        1) Rich in mitochondria
        2) Contains numerous vesicles filled with neurotransmitter molecules
    b. Outer segment
        1) Connected to inner segment by narrow stalk
        2) Packed with hundreds of flattened disks, stacked on one another
        3) Light-capturing photopigment molecules on membranes of these disks
4. Rhodopsin is rod cell photopigment
    a. Opsin protein coupled to molecule of *cis*-retinal — fig 55.21
    b. *Cis*-retinal produced from carotene
5. Photopsin is rod cell photopigment
    a. Three kinds of cones, each has *cis*-retinal plus opsin with slightly different amino acid sequence

b. Sequence shifts absorption maximum fig 55.22
   1) 500 nanometers in rhodopsin
   2) 455 nm is blue-absorbing
   3) 530 nm is green-absorbing
   4) 625 nm is red-absorbing
c. Different light-absorbing properties account for different cone color sensitivities

6. Many animals experience color vision
   a. Include vertebrates that are diurnal (active during day)
   b. Also insects
      1) Honeybees see light in near-ultraviolet range
      2) Invisible to human eye
   c. Some animals see color but with different system than humans
      1) Fish, turtles, and birds have four or five kinds of cones
      2) Extra cones used to see near-ultraviolet light
   d. Some mammals, like squirrels, have only two types of cones

B. Structure of the Retina
1. Retina composed of three layers of cells fig 55.23
   a. Rods and cones in layer closest to external surface of eyeball
   b. Next layer contains bipolar cells
   c. Layer closest to inside of eye composed of ganglion cells
2. Light must pass through ganglion and bipolar cells to reach retinal photoreceptors
   a. Rods and cones synapse with bipolar cells
   b. Bipolar cells synapse with ganglion cells
   c. Flow of sensory information is opposite the path of light
3. Retina contains two other types of neurons
   a. Horizontal cells and amacrine cells
   b. Synapse with other cells in a given layer of retina

C. Sensory Transduction in Photoreceptors
1. Sequence is inverse of events associated with other sensory stimuli
   a. Photoreceptors in the dark release inhibitory neurotransmitter
   b. Hyperpolarizes bipolar neurons
   c. When inhibited, do not release excitatory neurotransmitter to ganglion cells
   d. Light inhibits photoreceptors from releasing inhibitory neurotransmitter
   e. Light stimulates bipolar cells, ganglion cells, transmits action potentials to brain
2. Rod or cone contains many Na^+ channels in plasma membrane of outer segment
   a. In dark many channels are open
   b. Na^+ ions continually diffuse into outer segment, across stalk to inner segment
   c. Small flow in absence of light called the dark current
   d. Causes membrane to be somewhat depolarized in the dark
3. In the light, Na^+ channels in outer segment close rapidly
   a. Reduces dark current
   b. Causes photoreceptor to hyperpolarize
4. Cyclic GMP (cGMP) required to keep Na^+ channels open
   a. Channels close if cGMP converted to GMP
   b. *Cis*-retinal is converted to *trans*-retinal when the photopigment absorbs light
   c. Isomerization causes retinal to dissociate from opsin: Bleaching reaction
   d. Opsin protein changes shape
   e. Shape change activates G protein
   f. In turn activates hundreds of phosphodiester molecules
   g. This breaks down cGMP to GMP, close Na^+ channels
   h. Channels close at rate of 1000 per second, inhibit dark current

i. Single photon of light causes hyperpolarization, release of less inhibitory neurotransmitter
j. Without inhibition, bipolar cells activate ganglion cells
k. Ganglion cells transmit action potentials to brain

III. VISUAL PROCESSING IN THE VERTEBRATE RETINA

A. Interpretation of Signals from the Retina
1. Action potentials from ganglion cells relayed through thalamus
   a. Transmitted through lateral geniculate nuclei of thalamus
   b. Projected to occipital lobe of cerebral cortex fig 55.24
2. Brain interprets information as light in specific part of eye's receptive field
   a. Pattern of activity encodes point-to point map
   b. Retina and brain image objects in visual space
3. Frequency of impulses indicates light intensity at each point
4. Relative activity of ganglia cells attached to cones provides color information
5. Relationship between receptors, bipolar cells, and ganglion cells differs within retina
   a. In fovea
      1) Each cone connects to one bipolar cell, each to one ganglion cell
      2) Provides high visual acuity in fovea
   b. Outside fovea
      1) Many rods converge on single bipolar cell
      2) Many bipolar cells converge on single ganglion cell
      3) Permits summation of neural activity
      4) Peripheral vision is more sensitive to low levels of light, but less acute, no color
6. Fovea serves as inspector, periphery serves as detector
7. Color blindness
   a. Due to inherited lack of one or more types of cones
      1) Trichromats experience normal color vision
      2) Dichromats have only two types of cones
         a) Many lack red cones (protanopia)
         b) Difficult to distinguish red from green
   b. Trait carried on X chromosome, affects more men than women
      1) Men have only one X
      2) Women have two, can carry trait in recessive state

B. Binocular Vision
1. Visual images of vertebrate eyes
   a. Eyes on opposite sides of head, each sees object at different angle
   b. Parallax permits three-dimensional imaging, depth perception
2. Predators have eyes set in front of head to increase stereoscopic vision fig 55.23
3. Prey have eyes set on sides of head to enlarge total receptive field
   a. Depth perception less important
   b. Increased field of view more important
4. Most birds have laterally placed eyes, two foveas in each retina
   a. One fovea provides sharp frontal vision, like mammals
   b. Other fovea provides sharp lateral vision

55.5 Some vertebrates use heat, electricity, or magnetism for orientation

I. DIVERSITY OF SENSORY EXPERIENCES

A. Heat
1. Electromagnetic radiation with wavelengths longer than visible light
2. Infrared radiation (longer than red) detected as radiant heat
3. Not possessed by aquatic animals as water absorbs heat
4. Sensed by pit vipers (including rattlesnakes)
   a. Heat-detecting pit organs located on either side of the head fig 55.25
   b. Perceive heat emanating from motionless animals in complete darkness
      1) Pit organ composed of two chambers
      2) Organ operates by comparing temperatures of two chambers
      3) Nature of organ unknown, probably consists of temperature-sensitive neurons
   c. Two pit organs provide stereoscopic information, processed in visual center

B. Electricity
1. Not possessed by terrestrial animals, air does not conduct electricity
2. All aquatic animals generate electrical currents from muscle contractions
3. Electric fish have electrical discharges produced by special organs of modified muscle
   a. Use weak electrical charges to locate prey animals, mates
   b. Construct three-dimensional image of environment
4. Elasmobranchs (sharks, rays, skates) have special electroreceptors
   a. Receptors called ampullae of Lorenzini
   b. Located in sacs that open through jelly-filled canals to pores in body surface
   c. Jelly is good conductor
      1) Negative charge in canal opening depolarizes receptor at base
      2) Causes release of neurotransmitter, increased activity of sensory neurons
   d. Sharks can detect electrical fields generated in their prey
5. Teleost (bony) fish electroreception
   a. Lack ampullae of Lorenzini
   b. Some have electroreception via analogous structures
6. Duck-billed platypus evolved electroreceptors independently
   a. Receptors on bill detect electrical currents produced by muscles of shrimp and fish
   b. Animal can detect prey at night, in muddy water

C. Magnetism
1. Navigational, used by many birds, eels, sharks, and even bacteria
2. Birds in blind cages orient to the earth's magnetic fields
   a. Orientation does not occur in cages shielded by steel
   b. Orientation improper with artificially altered magnetic field
3. Nature of magnetic receptor poorly understood

INSTRUCTIONAL STRATEGY

PRESENTATION ASSISTANCE:

Stress the need for all types of sensory systems, not just those we associate with communication. Senses are needed to provide the brain with information so it can direct the motor systems.

Sensory systems are closely integrated with and adapted to the environment. Speculate on the changes that might occur with humans under different environmental conditions such as the silence and weightlessness associated with space.

Discuss how hearing and olfaction are altered with colds and allergies.