

Biosystems II: Neuroscience

Sensory Systems

Lecture 2

Audition, Vision, Proprioception

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Outline

1. Auditory receptors

- a) The structure of the inner ear (Fig.2-1)
- b) The basilar membrane is a mechanical analyzer of sound frequency (Fig.2-2)
- c) Hair cells transform mechanical energy into neural signals (Fig.2-3, 2-4, 2-5)

2. Visual receptors

- a) The retina contains the eye's receptor sheet (Fig.2-6, 2-7)
- b) Two types of photoreceptors, rods and cones, are differentially distributed across the retina (Fig.2-8)
- c) Separate functional roles of rods and cones (Fig.2-9)
- d) Cones mediate color vision (Fig.2-10)
- e) Phototransduction results from a three-stage cascade of biochemical events in the photoreceptors (Fig.2-11)
- f) Transduction of visual signal differs from other sensory transduction: hyperpolarization instead of depolarization (Fig.2-12)

3. Somatic receptors

- a) Somatosensory system has a large number of receptors (Fig.2-13A,B)
- b) Mechanoreceptors vary in the receptive field (RF) size and their distributions (Fig.2-14, 2-15)
- c) Spatial discrimination threshold is related to the size of RF (Fig.2-16)
- d) Mechanoreceptors also differ in their sensitivity to vibrations (Fig.2-17)

The structure of the inner ear. The cochlea, viewed face-on (upper left) and in cross section (subsequent panels). The stapes transfers force from the tympanic membrane to the oval window. The hair cells are named for their tufts of stereocilia; inner hair cells receive afferent inputs from the VIII nerve, whereas outer hair cells receive mostly efferent input. As a result, the round window bulges out-ward when the stapes compresses the oval window, thus deforming the basilar membrane, which in turn deflects the stereocilia of the hair cells. The only point of fluid continuity between the scala vestibule and scala tympani is at the helicotrema. The cross sections show the scala media between the scala vestibule and scala tympani; the hair cells are located between the basilar and tectorial membranes.

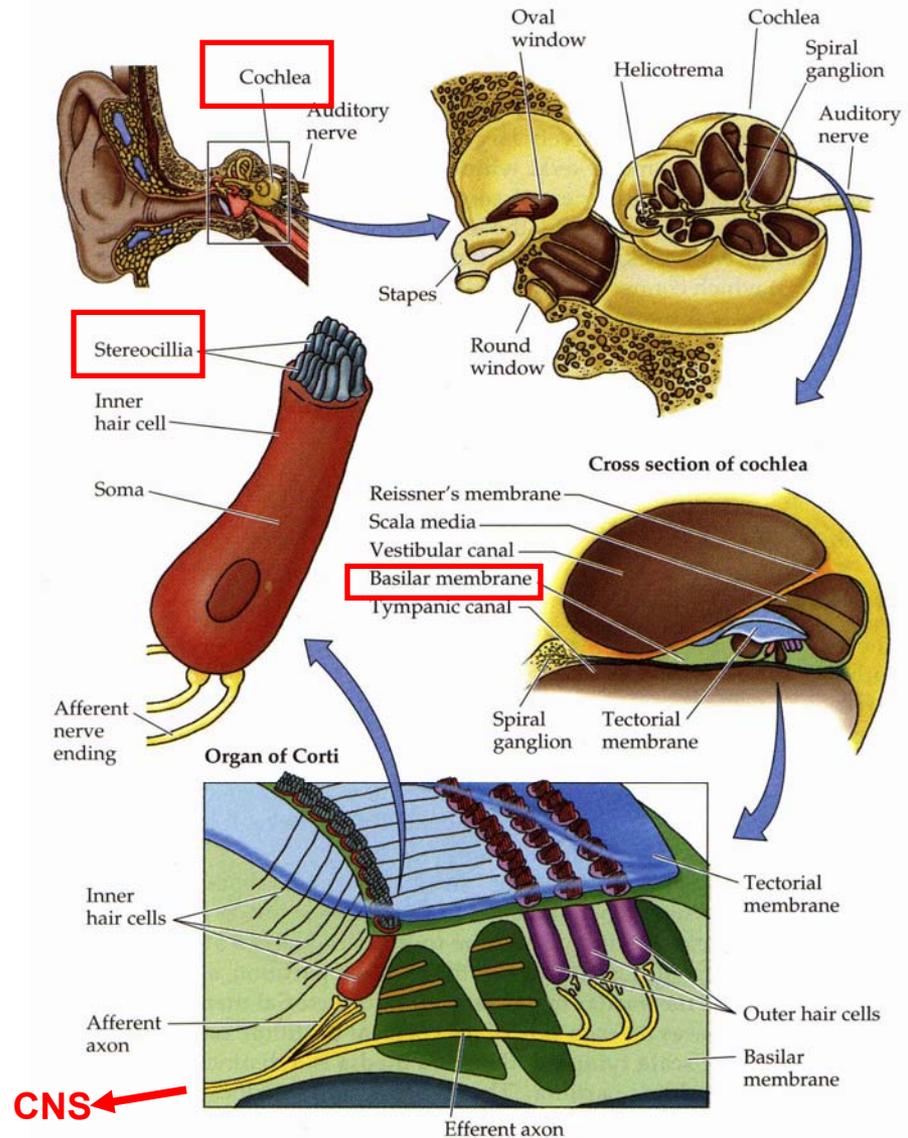
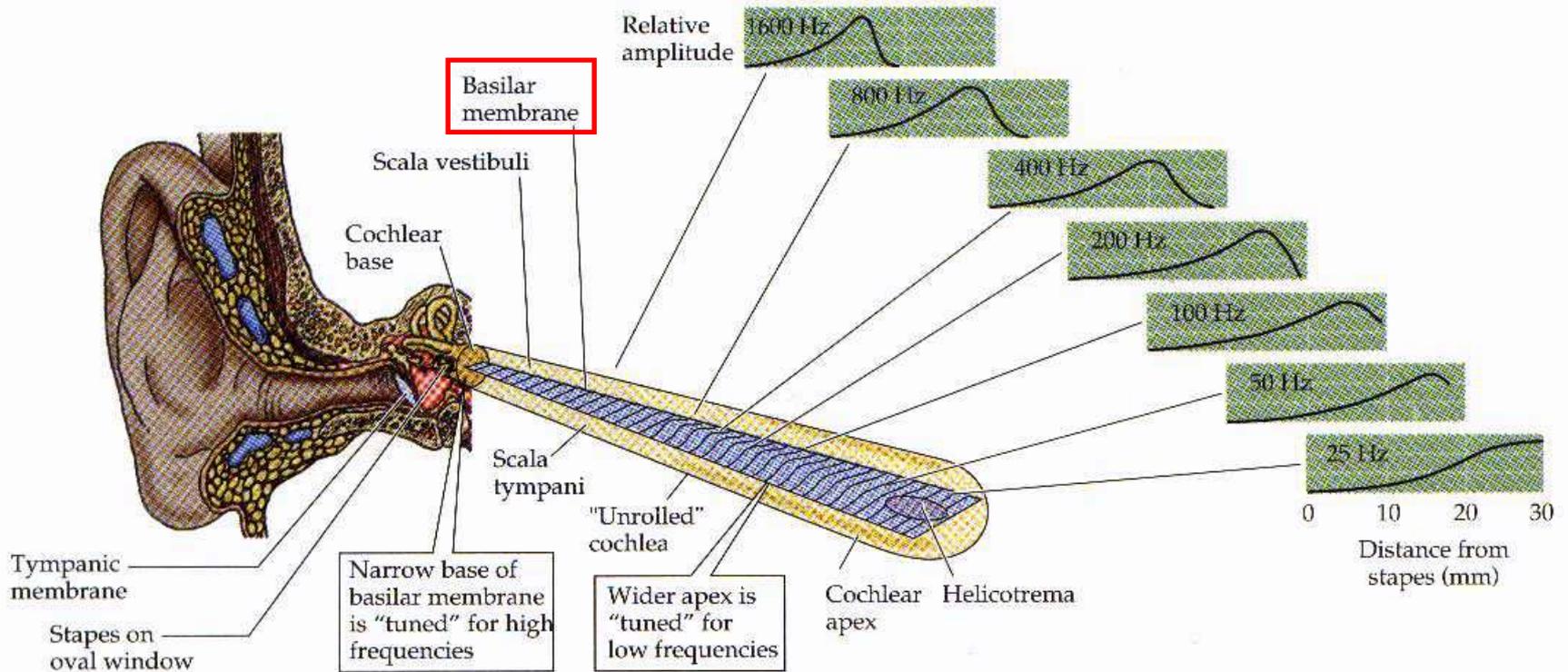
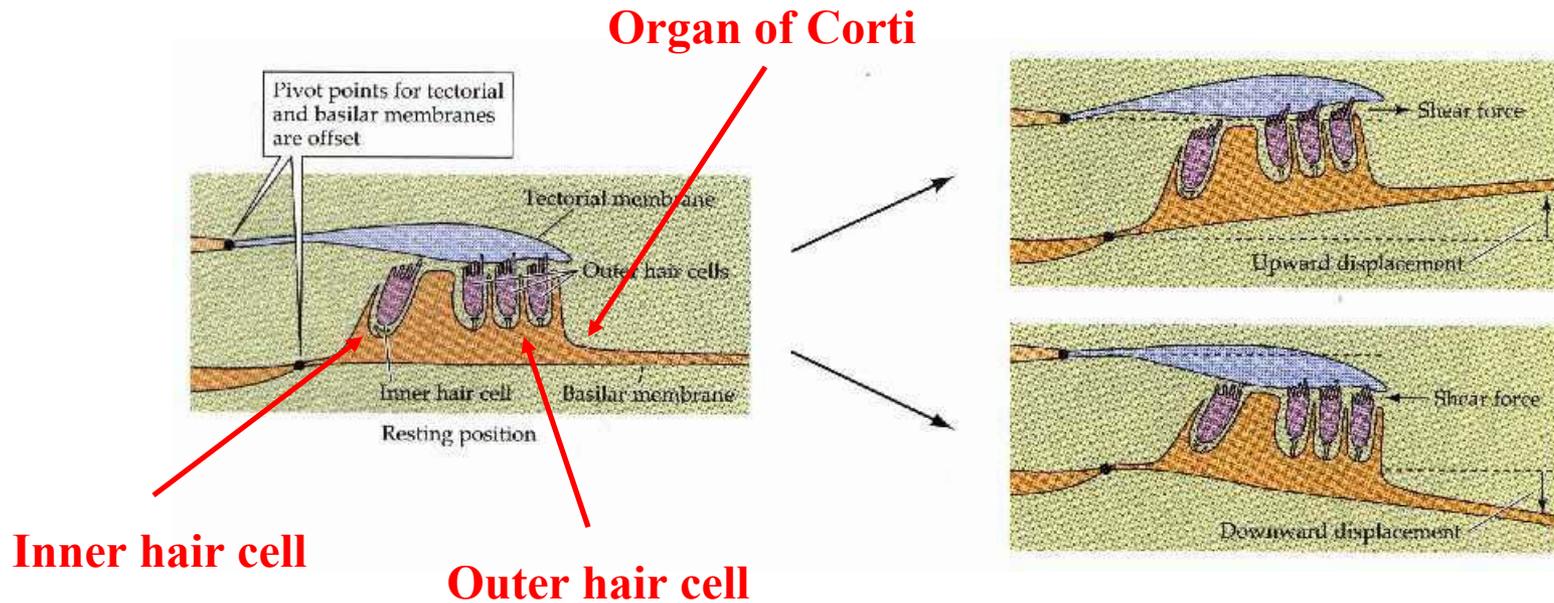


Fig.2-1



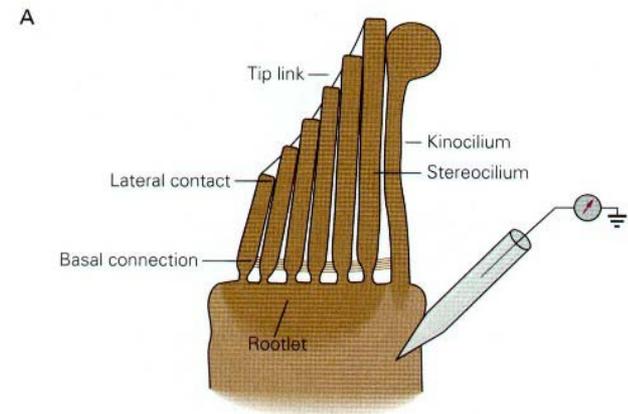
The basilar membrane is a mechanical analyzer of sound frequency. Traveling waves along the cochlea, A traveling wave is shown at a given instant along the cochlea, which has been uncoiled for clarity. The graphs profile the amplitude of the traveling wave along the basilar membrane for different frequencies, and show that the position where the traveling wave reaches its maximum amplitude varies directly with the frequency of stimulation.,

The organ of Corti and hair cells



Hair cells transform mechanical energy into neural signals. Movement of the basilar membrane creates a shearing force that bends the stereocilia of the hair cells. The pivot point of the basilar membrane is off- set from the pivot point of the tectorial membrane, so that when the basilar membrane is displaced, the tectorial membrane moves across the tops of the hair cells, bending the stereocilia,

Mechanoelectrical Transduction by Hair Cells



Mechanical sensitivity of a hair cell.

A. A schematic drawing of a hair cell with a recording electrode inserted into its cytoplasm.

B. Application of a mechanical force to the hair bundle deflects this elastic structure.

C. When the top of a hair bundle is displaced back and forth by a stimulus probe (lower trace), the opening and closing of mechanically sensitive channels produces an oscillatory receptor potential (upper trace).

D. The sigmoidal relation between hair-bundle deflection (abscissa) and receptor potential (ordinate) is a stimulated hair cell.

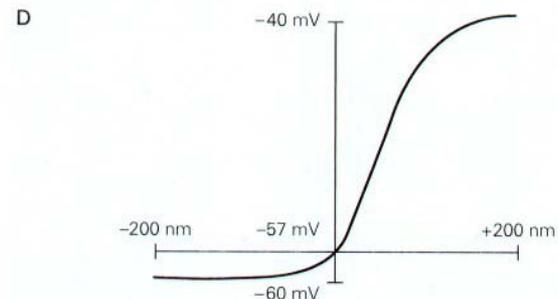
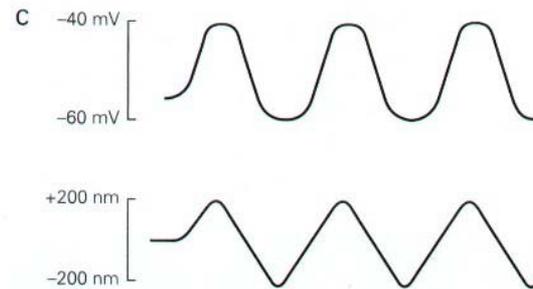
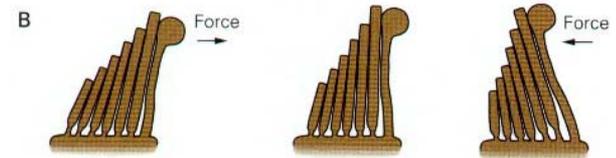


Fig.2-4

Mechanoelectrical Transduction by Hair Cells (cont.)

A model for the mechanism of mechano-electrical transduction by hair cells.

A. Top: The ion channels that participate in mechanoelectrical transduction in hair cells are gated by elastic structures in the hair bundle. The channel is assumed to be a membrane-spanning protein with a cation-selective pore. Ion permeation through this channel is regulated by a molecular gate, whose opening and closing is controlled by the tension in an elastic element, the gating spring, that senses hair-bundle displacement. (Adapted from Howard and Hudspeth 1988.)
Bottom: When the hair bundle is at rest each transduction channel clatters between closed and open states, spending most of its time shut (left). Displacement of the bundle in the positive direction increases the tension in the gating spring, here assumed to be a tip link, attached to each channel's molecular gate (middle). The enhanced tension promotes channel opening and the influx of cations, thereby producing a depolarizing receptor potential (right).

B. The links that connect each stereociliary tip to the side of the longest adjacent stereocilium are visible in this scanning electron micrograph of a hair bundle's top surface (left) and transmission electron micrograph (right). Although each tip link is only 3 nm in diameter, the links appear stouter in the illustration on the left because of metallic coating during specimen preparation.

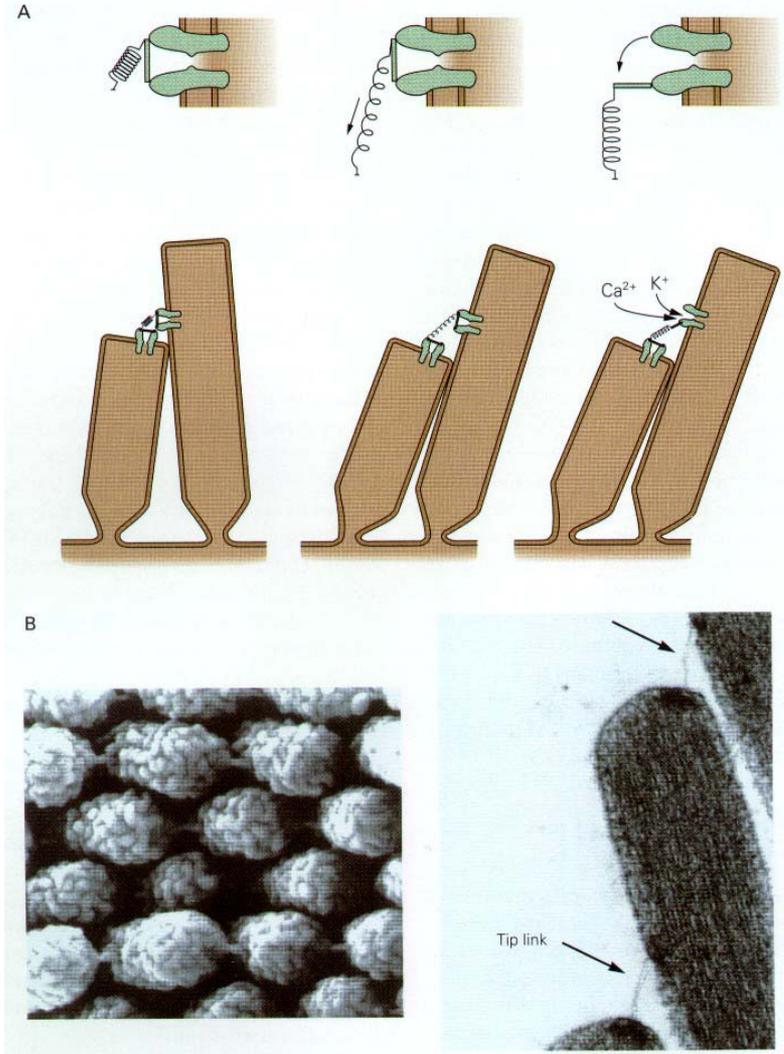
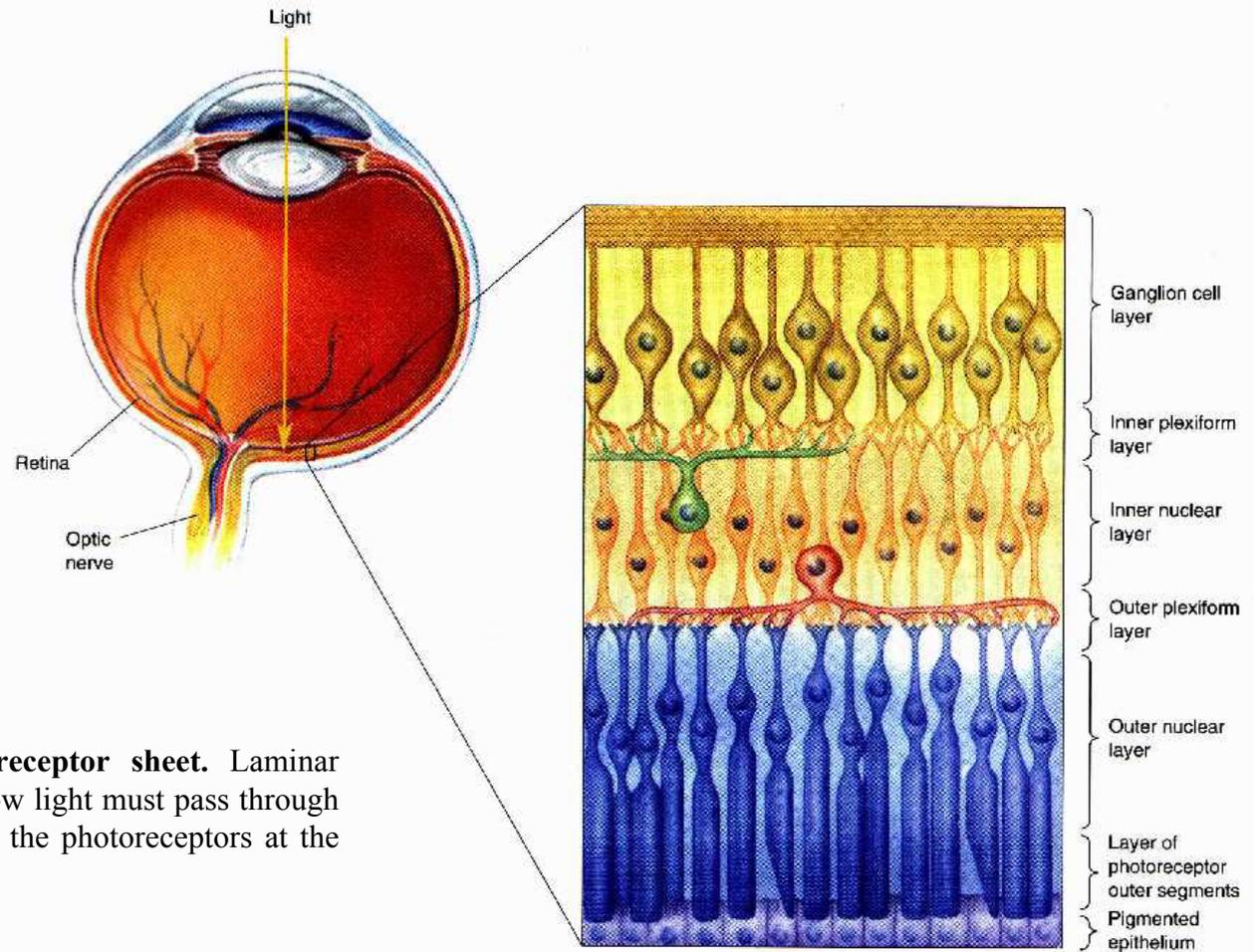
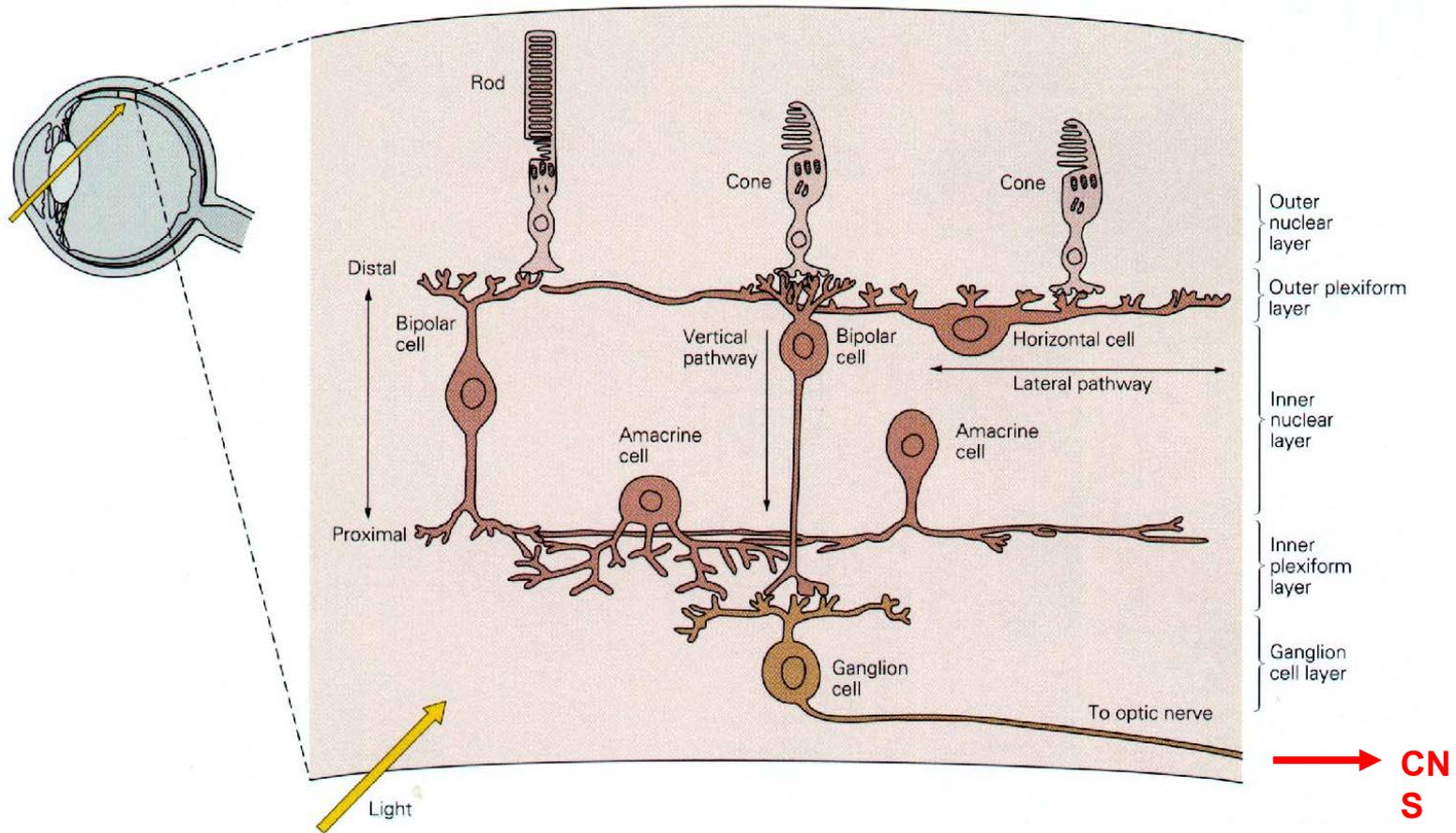


Fig.2-5

The retina contains the eye's receptor sheet



The retina contains the eye's receptor sheet. Laminar organization of the retina. Notice how light must pass through several cell layers before it reaches the photoreceptors at the back of the retina.



The retina has three major functional classes of neurons. Photoreceptors (rods and cones) lie in the outer nuclear layer, interneurons (bipolar, horizontal, and amacrine cells) in the inner nuclear layer, and ganglion cells in the ganglion cell layer. Photoreceptors, bipolar cells, and horizontal cells make synaptic connections with each other in the outer plexiform layer. The bipolar, amacrine, and ganglion cells make contact in the inner plexiform layer. Information flows vertically from photoreceptors to bipolar cells to ganglion cells, as well as laterally via horizontal cells in the outer plexiform layer and amacrine cells in the inner plexiform layer

Fig.2-7

Regional difference in retinal structure

Two types of photoreceptors, rods and cones, are differentially distributed across the retina. Regional differences in retinal structure. (a) Cones are found primarily in the central retina, within 10 degree of the fovea. Rods are absent from the fovea and are found mainly in the peripheral retina. (b) In the central retina, relatively few photoreceptors feed information directly to a ganglion cell; in the peripheral retina, many photoreceptors provide input. This arrangement makes the peripheral retina better at detecting dim light but the central retina better for high-resolution vision.

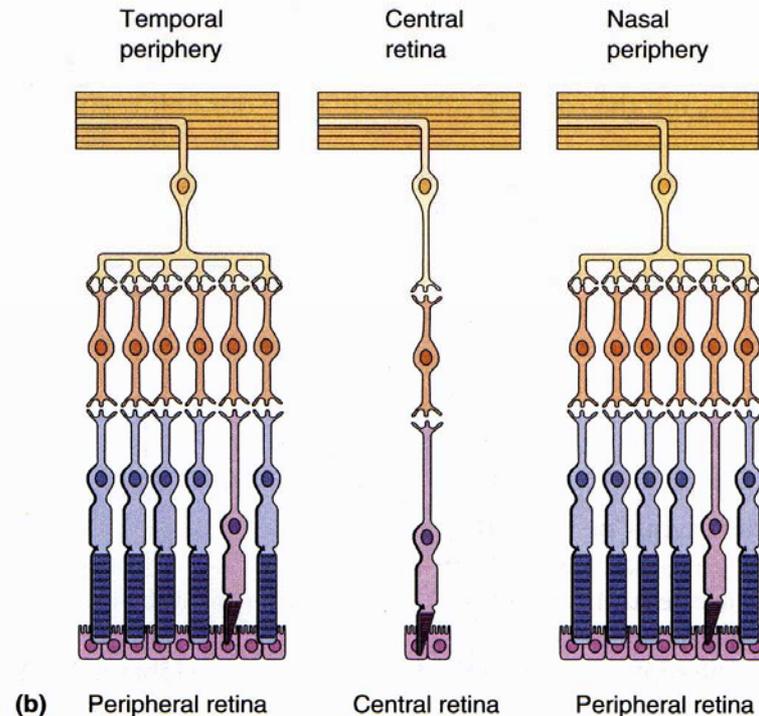
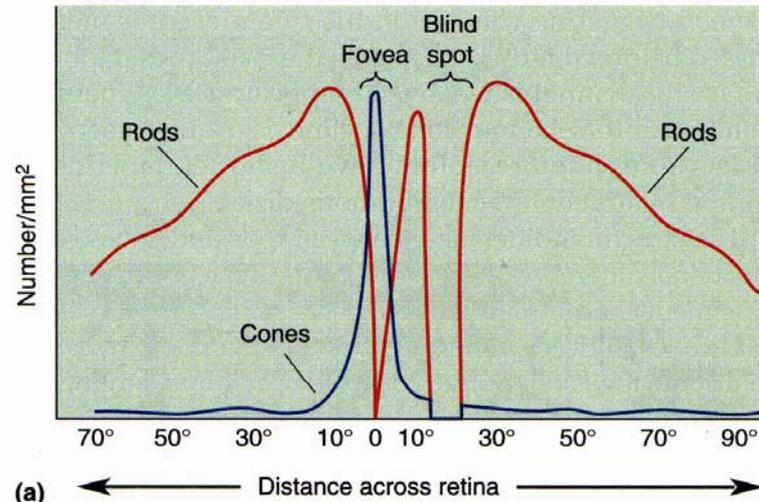


Fig.2-8

Separate functional roles of rods and cones

Rods	Cones
<p>High sensitivity, specialized for night vision:</p> <ul style="list-style-type: none"> More photopigment, capture more light High amplification, single photon detection Saturate in daylight <p>Low temporal resolution:</p> <ul style="list-style-type: none"> Slow response, long integration time <p>More sensitive to scattered light</p>	<p>Lower sensitivity, specialized for day vision:</p> <ul style="list-style-type: none"> Less photopigment Less amplification Saturate only in intense light <p>High temporal resolution:</p> <ul style="list-style-type: none"> Fast response, short integration time <p>Most sensitive to direct axial rays</p>
Rod system	Cone system
<p>Low acuity: highly convergent retinal pathways, not present in central fovea</p> <p>Achromatic: one type of rod pigment</p>	<p>High acuity: less convergent retinal pathways, concentrated in fovea</p> <p>Chromatic: three types of cones, each with a different pigment that is more sensitive to a different part of the visible spectrum</p>

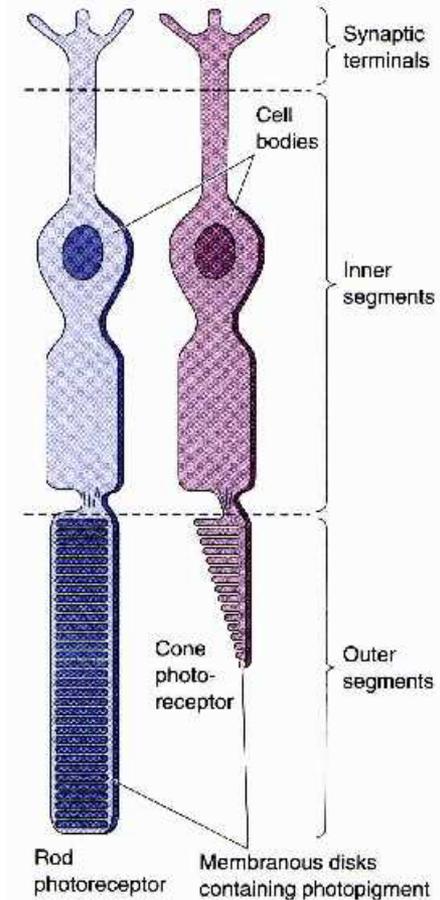
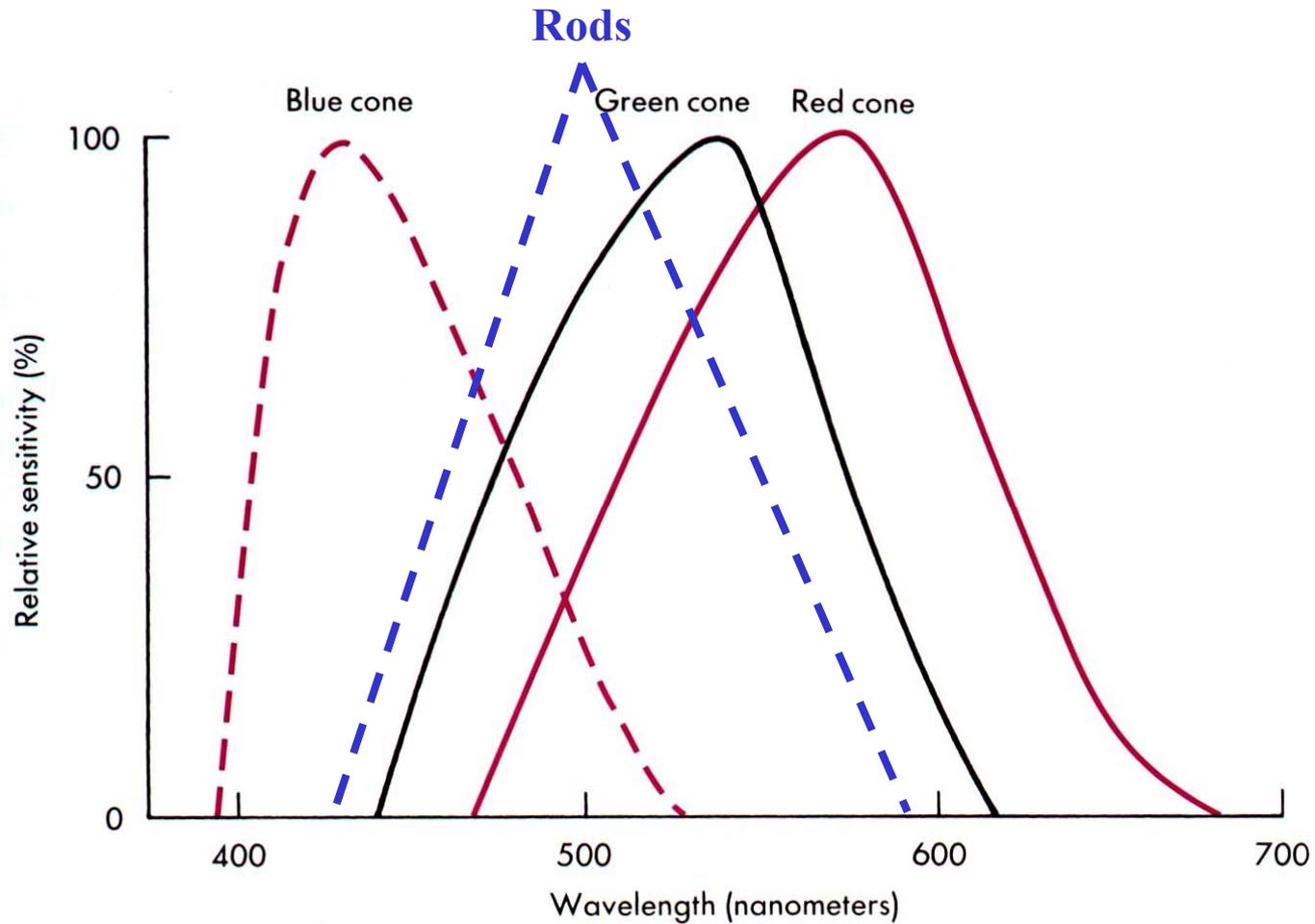


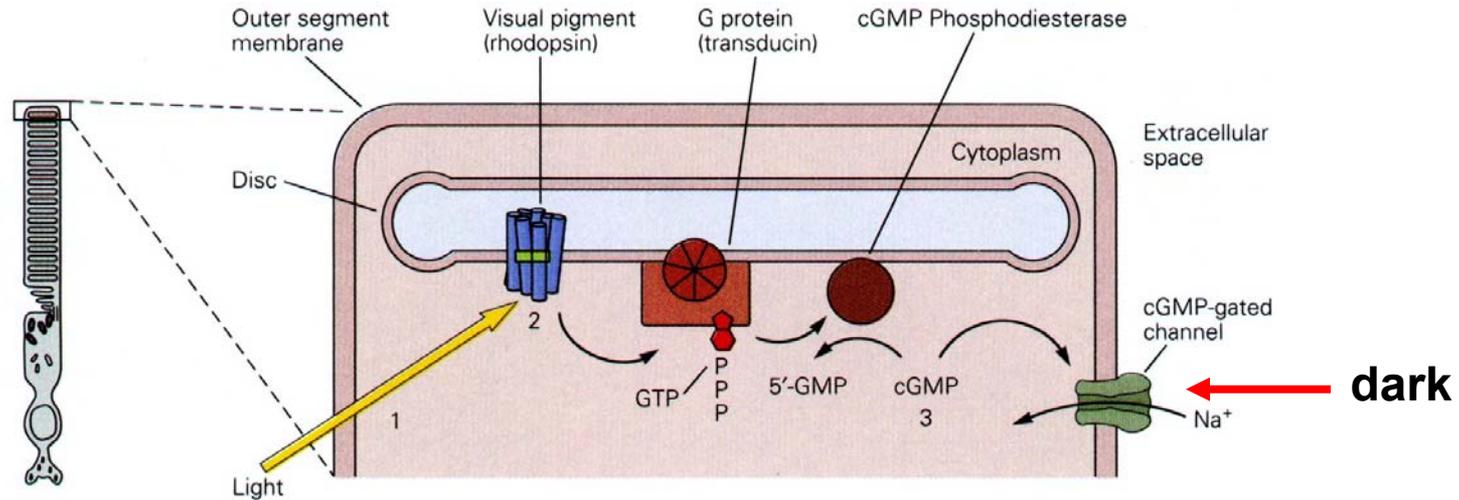
Fig.2-9

Cones mediate color vision

The spectral sensitivity of the three types of cones in the human retina is shown. Note that the curves overlap



Phototransduction results from a three-stage cascade of events

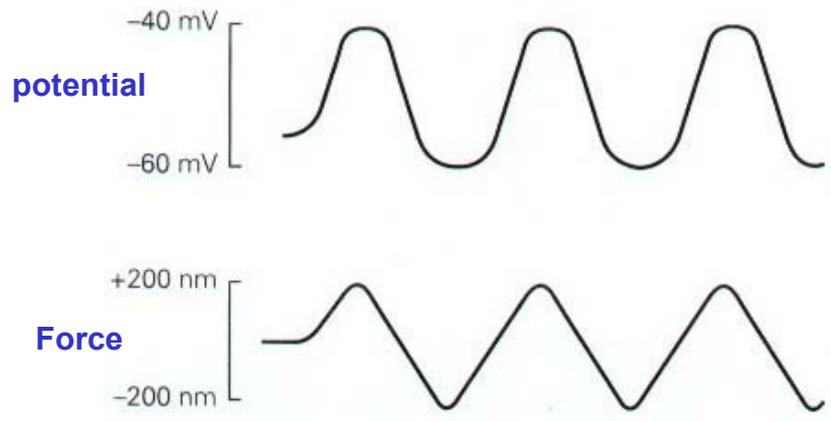
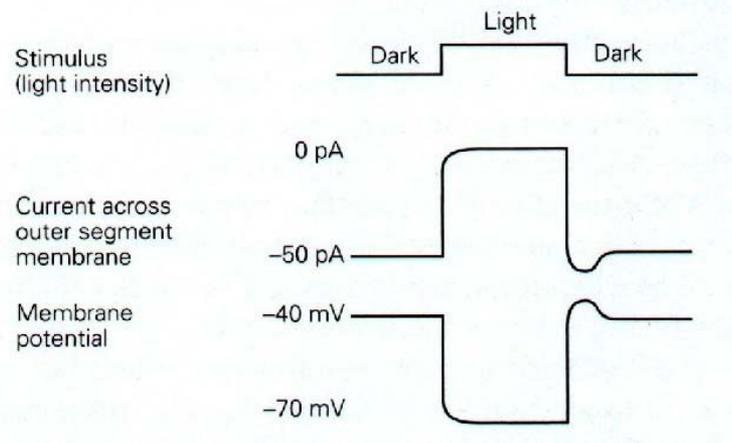
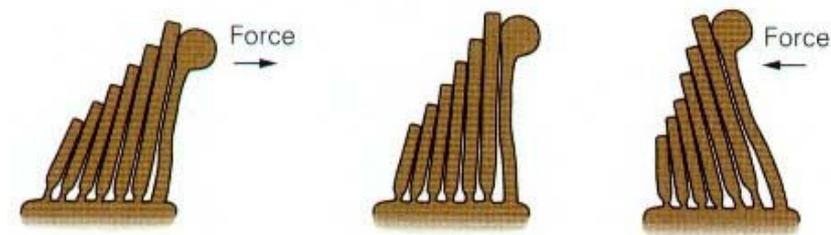
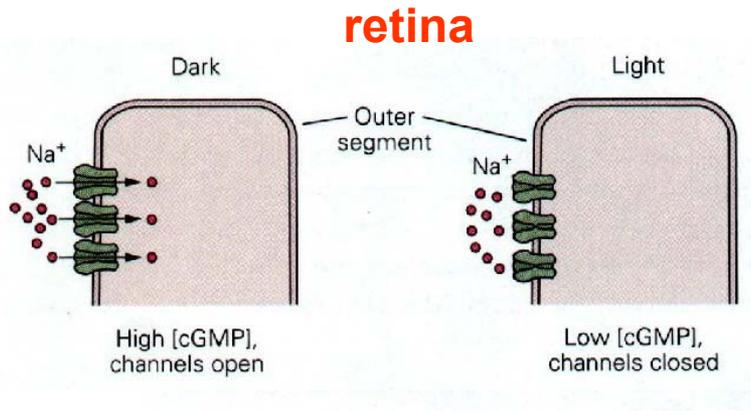


Stage-1: Light is absorbed by visual pigment (*rhodopsin* in rods) and activates pigment molecules

Stage-2: Activation of pigment molecules reduces the cytoplasmic concentration of cyclic GMP

Stage-3: The reduction in cGMP concentration closes cGMP-gated ion channels, thus **hyperpolarizing** the photoreceptor

Phototransduction results from a three-stage cascade of biochemical events in the photoreceptors. Phototransduction involves the closing of cation channels in the outer segment of the photoreceptor membrane. In the absence of light these cation channels are kept open by intracellular cGMP and conduct an inward current, carried largely by Na^+ . When light strikes the photoreceptor (illustrated here by a rod cell) the cGMP-gated channels are closed by a three-step process. (1) Light is absorbed by and activates pigment molecules (rhodopsin in rods) in the disc membrane (the green rectangle in the rhodopsin molecule represents the light-absorbing portion, retinal). (2) The activated pigment stimulates a G protein (transducin in rods), which in turn activates cGMP phosphodiesterase. This enzyme catalyzes the breakdown of cGMP to 5'-GMP. (3) As the cGMP concentration is lowered, the cGMP-gated channels close, thereby reducing the inward current and causing the photoreceptor to hyperpolarize.



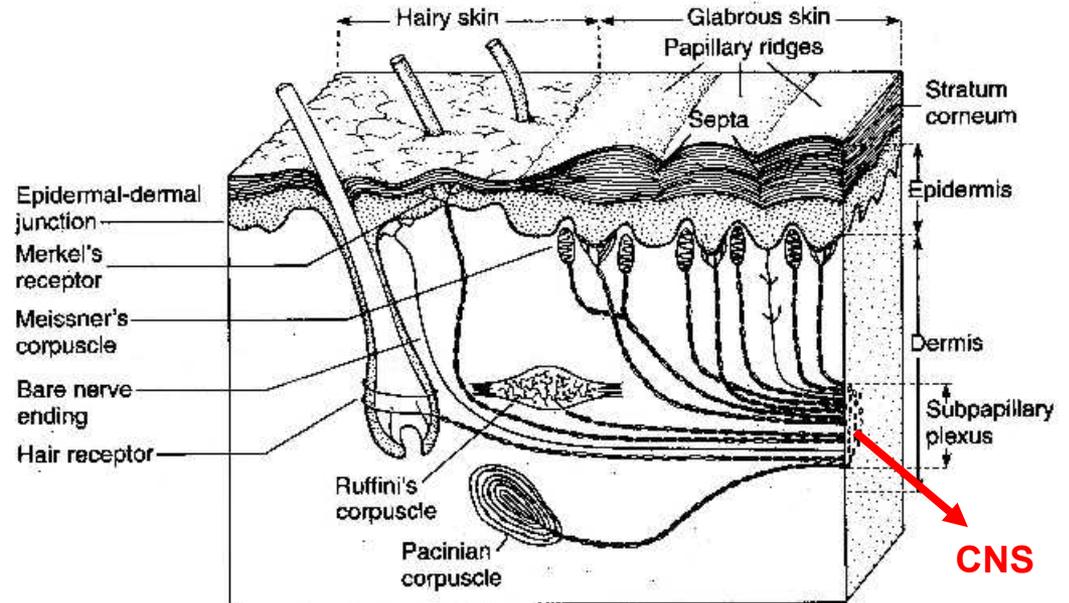
Transduction of visual signal differs from other sensory transduction: hyperpolarization instead of depolarization.

(upper left) A reduction in the cytoplasmic concentration of cGMP closes the cGMP-gated channels.

(lower left) An inward current of -50 pA is suppressed by a bright light, hyperpolarizing the cell to -70 mV, the equilibrium potential for K⁺. A light of intermediate intensity would hyperpolarize the cell to potentials between -40 and -70 mV.

Receptors in Somatosensory System

Receptor type	Fiber group	Quality
<i>Nociceptors</i>		
Mechanical	A δ	Sharp, pricking pain
Thermal and mechano-thermal	A δ	Sharp, pricking pain
Thermal and mechano-thermal	C	Slow, burning pain
Polymodal	C	Slow, burning pain
<i>Cutaneous and subcutaneous mechanoreceptors</i>		
Meissner's corpuscle	A β	Flutter
Pacinian corpuscle ¹	A β	Vibration
Ruffini corpuscle	A β	Steady skin indentation
Merkel receptor	A β	Steady skin indentation
Hair-guard	A β	Flutter
Hair-tylotrich	A β	
Hair-down	A δ	
<i>Muscle and skeletal mechanoreceptors</i>		
Muscle spindle primary	A α	Limb proprioception
Muscle spindle secondary	A β	Limb proprioception
Joint capsule mechanoreceptors	A β	Joint capsule pressure, limited role in limb proprioception
Golgi tendon organ	A α	



Somatosensory system has a large number of receptors. The location of various receptors in hairy and hairless (glabrous) skin of primates. Receptors are located in the superficial skin, at the junction of the dermis and epidermis, and more deeply in the dermis and in subcutaneous tissue. The receptors of the glabrous skin are: Meissner's corpuscles, located in the dermal papillae, Merkel's receptors, also located in the dermal papillae, and bare nerve endings. The receptors of the hairy skin are: hair receptors, Merkel's receptors (having a slightly different organization than their counterparts in the glabrous skin), and bare nerve endings. Subcutaneous receptors, beneath both glabrous and hairy skin, include pacinian and Ruffini's corpuscles. .

Mechanoreceptors in glabrous skin vary in the size and structure of their receptive fields. Each colored area on the hands indicates the receptive field of a different sensory nerve fiber in the human median nerve.

A. The Merkel disk receptor in the superficial skin and the subcutaneous Ruffini ending are slowly adapting receptors. The Merkel disk receptor has a small, highly localized receptive field, whereas the Ruffini ending has a large field (light purple) with a central zone of maximal sensitivity (dark purple). Depending on their location, individual Ruffini endings are excited by stretch of the skin in specific directions as indicated by arrows.

B. The Meissner's corpuscle in the superficial skin and the subcutaneous Pacinian corpuscle are rapidly adapting receptors. Meissner's corpuscles on the fingertips have receptive fields averaging 2-3 mm in diameter, while receptive fields on the palm average 10 mm in diameter. The receptive fields of Pacinian corpuscles cover larger continuous surfaces on the fingers or palm (light pink) but have a central zone of maximal sensitivity located directly above the receptor (red).

C. Expanded view of the receptive fields of mechanoreceptors in the superficial and deep layers of glabrous skin. The relative sensitivity to pressure is shown as a contour map in which the most sensitive regions are indicated in red and the least sensitive areas in pale pink. Receptive fields in the superficial layers of the skin have many points of high sensitivity, marking the positions of the Meissner's corpuscles or Merkel disk receptors. Receptive fields in the deep layers have a single point of maximal sensitivity overlying the Pacinian or Ruffini receptor.

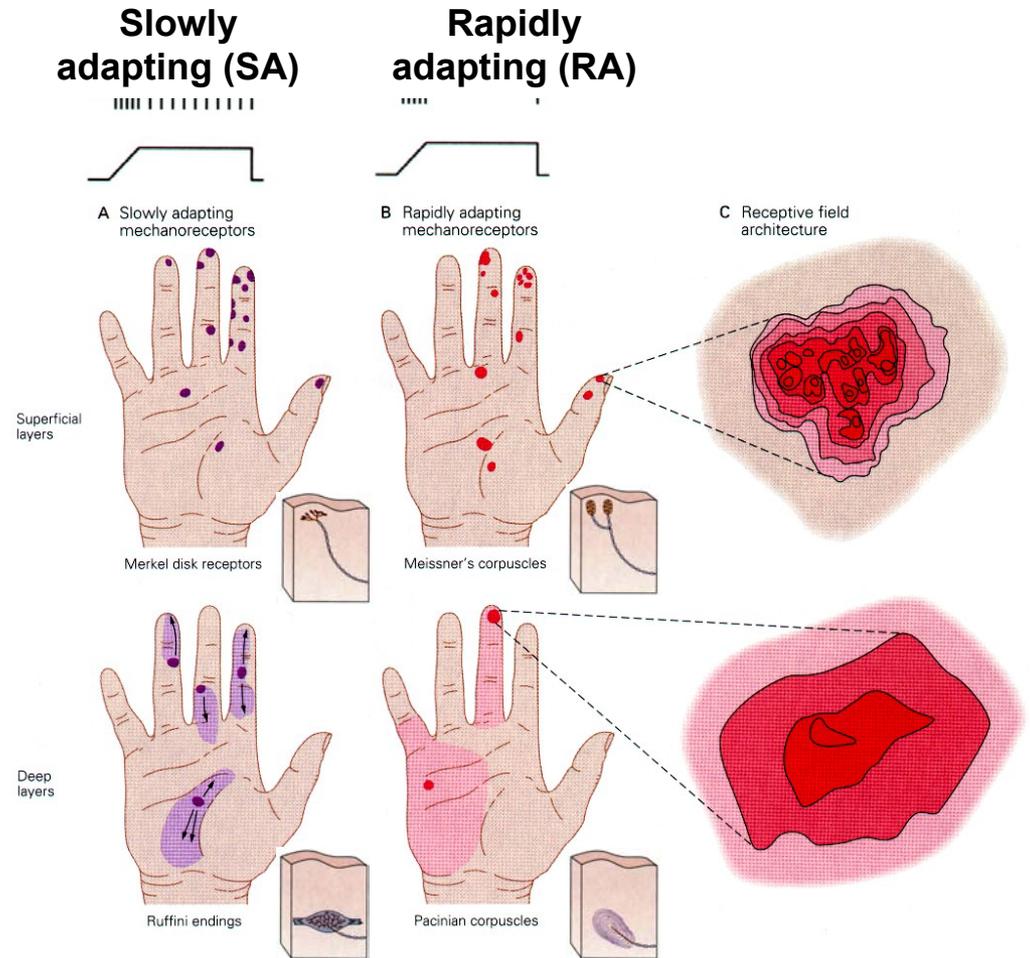
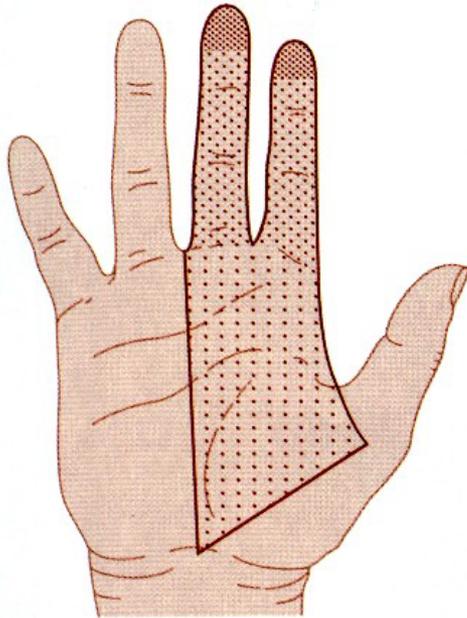


Fig.2-14

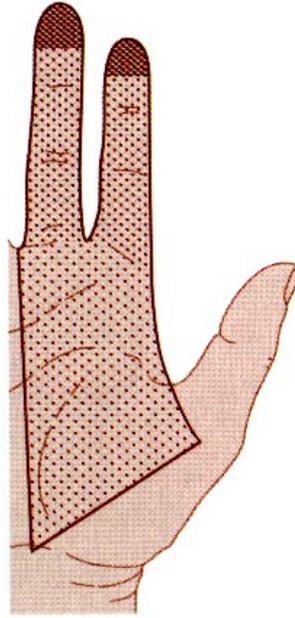
Superficial layers

Deep layers

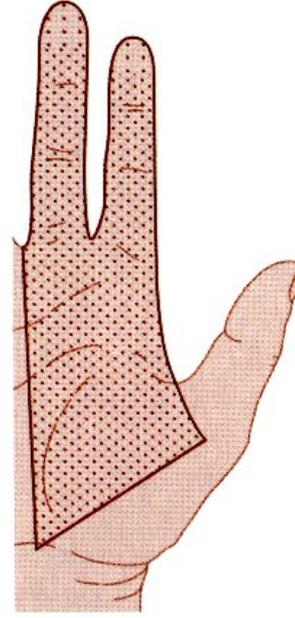
SA I (Merkel)



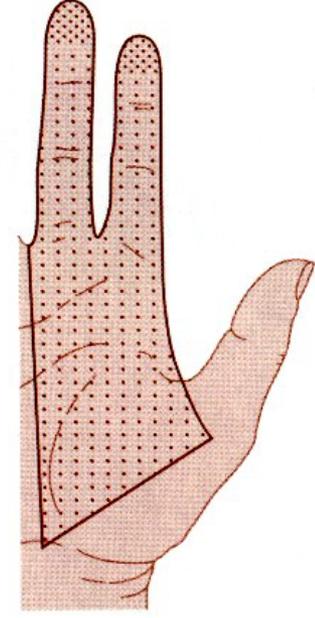
RA (Meissner's)



SA II (Ruffini)



PC (Pacian)



The distribution of receptor types in the human hand varies. The number of sensory nerve fibers innervating an area is indicated by the stippling density, with the highest density of receptors shown by the heaviest stippling. (RA = rapidly adapting, SA = slowly adapting.) Meissner's corpuscles (RA) and Merkel disk receptors (SA I) are the most numerous receptors; they are distributed preferentially on the distal half of the fingertip. Pacinian corpuscles (PC) and Ruffini endings (SA II) are much less common; they are distributed more uniformly on the hand, showing little differentiation of the distal and proximal regions. The fingertips are the most densely innervated region of skin in the human body, receiving approximately 300 mechanoreceptive nerve fibers per square centimeter. The number of mechanoreceptive fibers is reduced to 120/cm² in the proximal phalanges, and to 50/cm² in the palm.

Spatial discrimination threshold is related to the size of RF

Two-point discrimination varies throughout the body surface. The two-point threshold measures the minimum distance at which two stimuli are resolved as distinct. At smaller separations the stimuli are blurred into a single continuous sensation spanning the distance between the points. Two-point thresholds are measured clinically using a calibrated compass in which the separation of the tips is accurately scaled. Two-point thresholds can also be determined from measurements of the ability of subjects to discriminate the orientation of grating ridges as a function of their spacing. This method measures spatial acuity more accurately. The two-point threshold varies for different body regions; it is about 2 mm on the finger tip but increases to 10 mm on the palm and 40 mm on the arm. The two-point thresholds highlighted in pink match the diameter of the corresponding receptive fields shown in pink on the body. The greatest discriminative capacity is afforded in the finger tips, lips, and tongue, which have the smallest receptive fields.

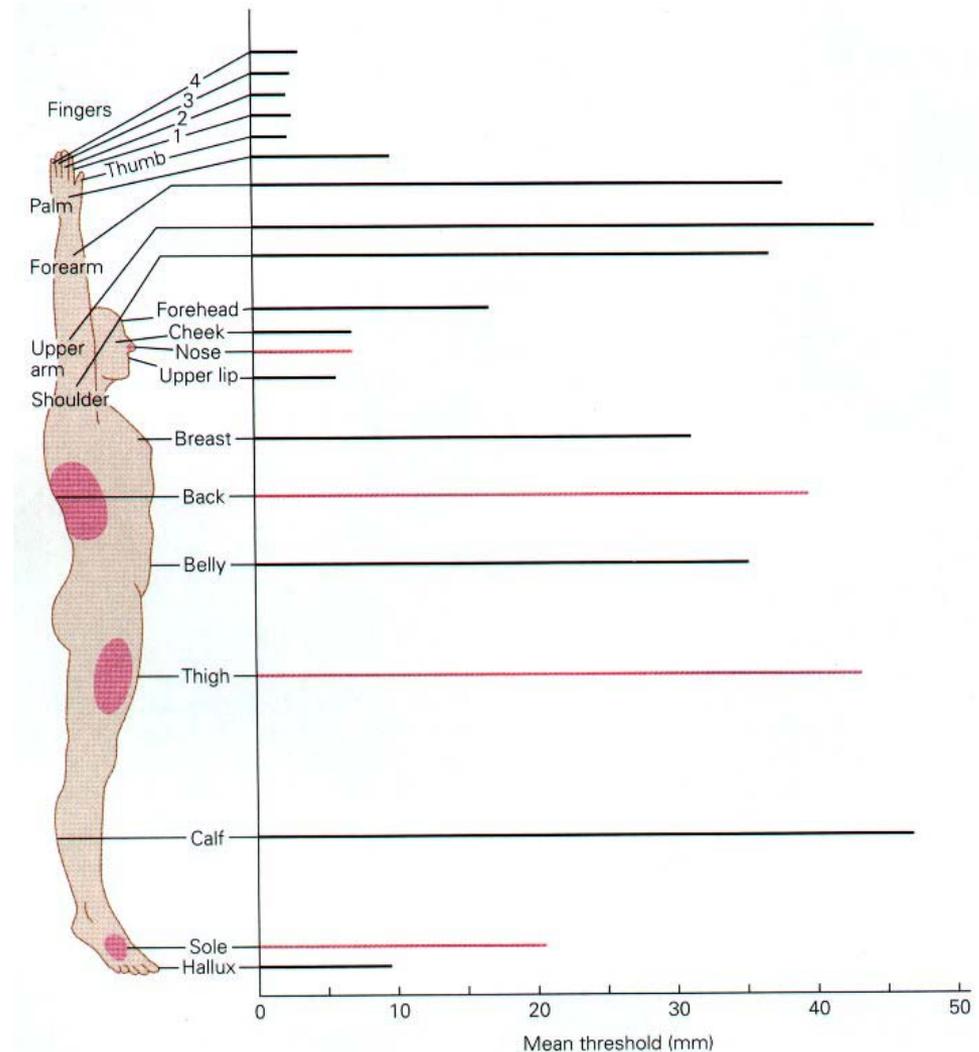
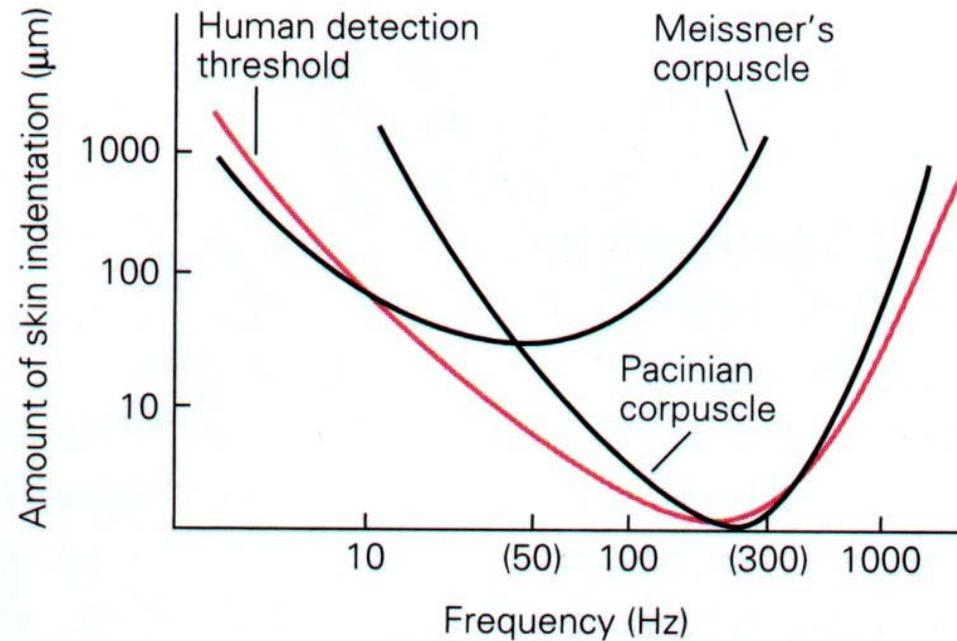
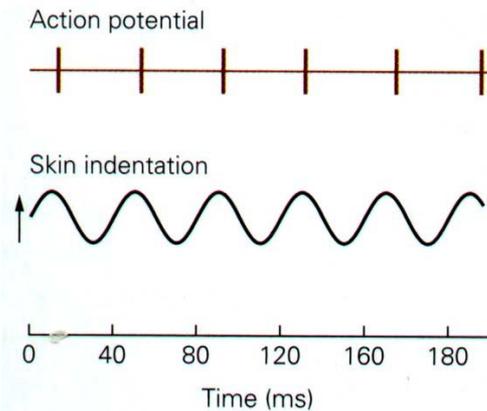


Fig.2-16

Mechanoreceptors also differ in their sensitivity to vibrations



A rapidly adapting mechanoreceptor responds to sinusoidal mechanical stimuli with a single action potential for each cycle. The record here is for a receptor stimulated with a 25 Hz vibratory stimulus; the firing frequency of the receptor is 25 action potentials per second. The lowest stimulus intensity that evokes one action potential per cycle of the sinusoidal stimulus is called the receptor's "tuning threshold". The threshold for detecting vibration corresponds to the tuning threshold of the mechanoreceptor. The sensitivity threshold for Meissner's corpuscles is lowest for frequencies of 20-50 Hz. Pacinian corpuscles sense higher frequencies..

Comparison between modalities

Auditory:

Inner hair cell

Outer hair cell

Visual:

Rods

Cones

Somatic:

Mechanoreceptors
(indentation, vibration)

Nociceptors

(thermal, pain)

Summary of Lecture 2

- A sensory stimulus is coded by an array of receptors
- Subsets of receptors encode different stimulus attributes within each modality

Readings:

Principles of Neural Science, by E.R. Kandel, J.H. Schwartz and T.M. Jessell, 2000. 4th Ed. (Chapter 22, 26, 31)