Light reception

- Photoreceptors
  - Structure
  - Function
- Eye evolution
- Neural connections
- Color perception
- Optimizing vision
- Reading: Ch. 9 except pp 262-264

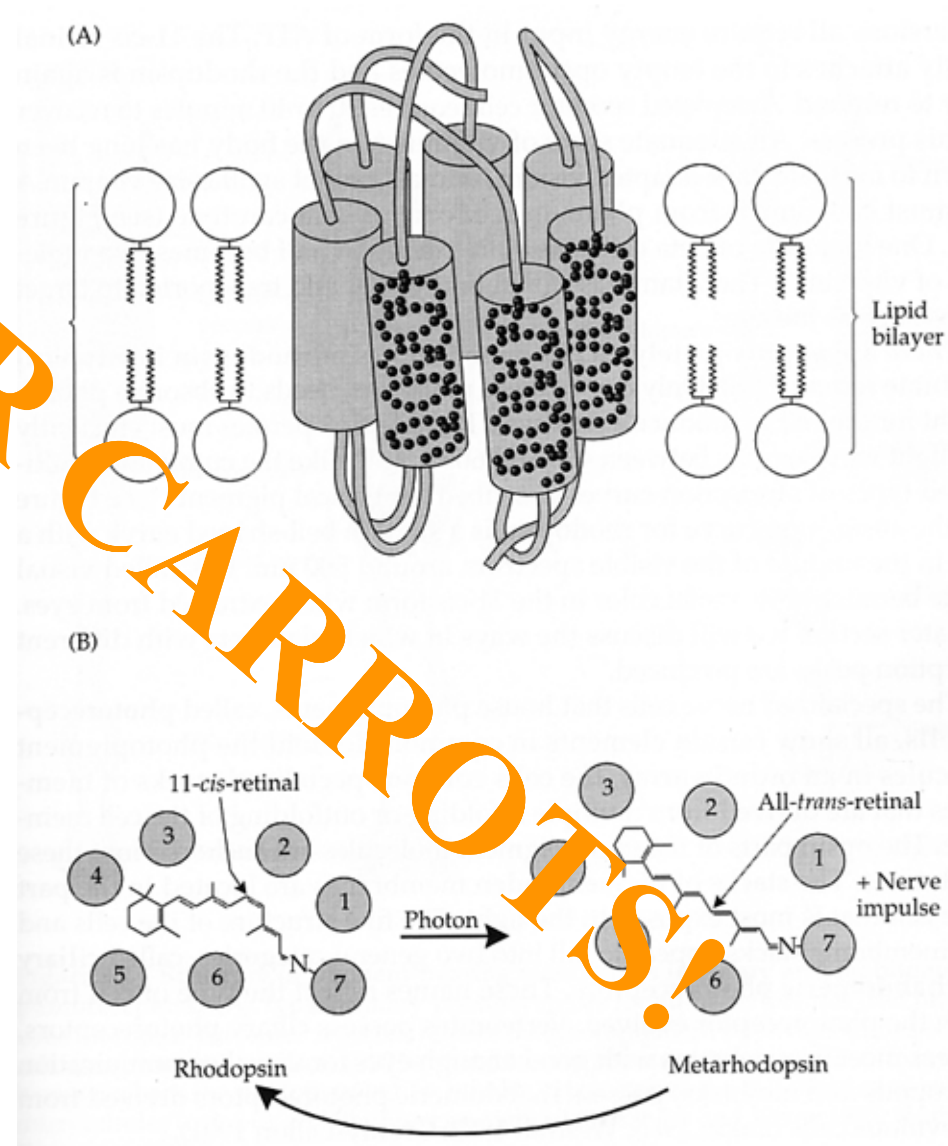
Rhodopsin

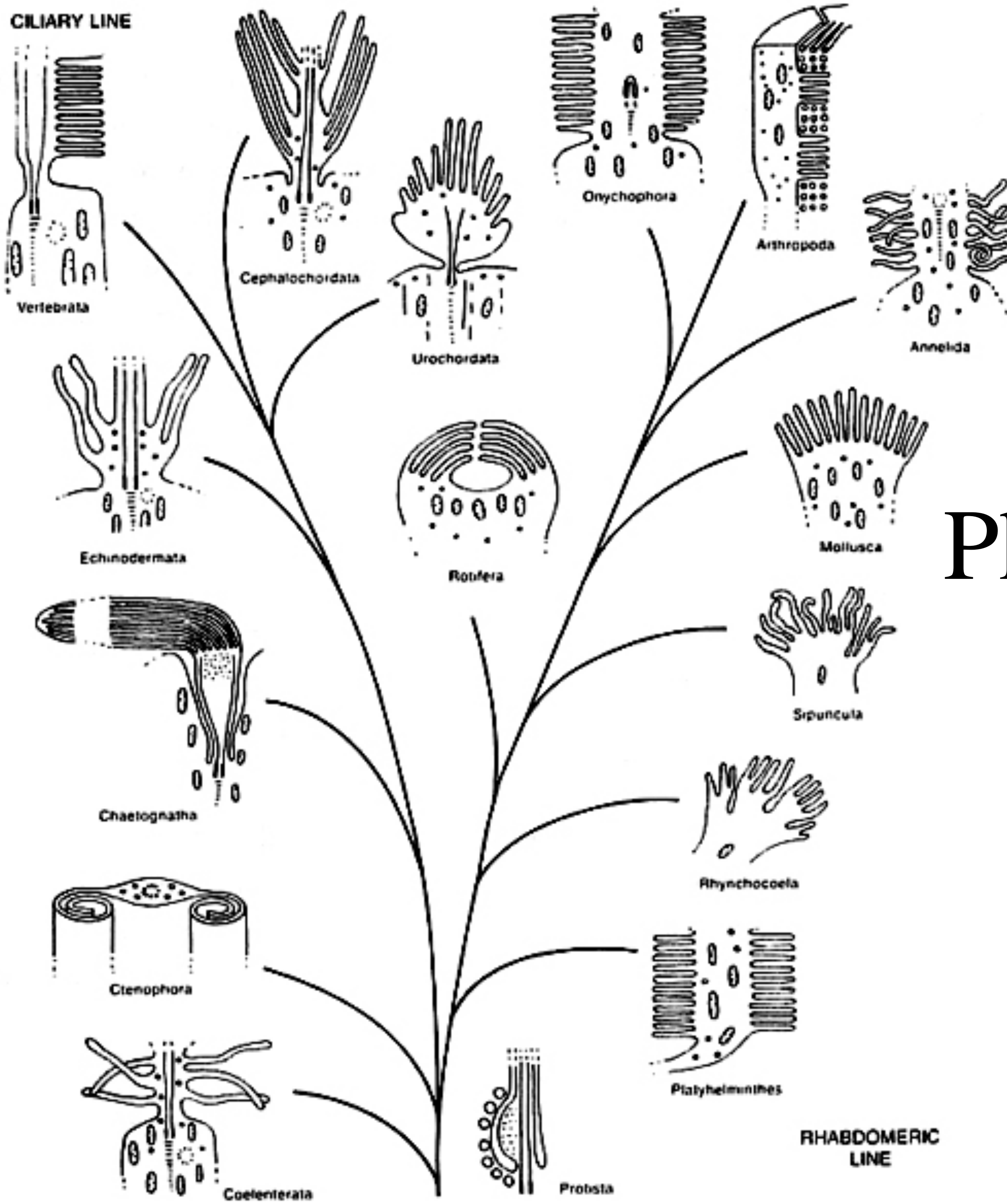
EAT YOUR CARROTS!

Opsin - 40 kD protein bound to membrane of photoreceptor cell

Rhodopsin - retinal bound to opsin. Retinal is derived from vitamin A which comes from splitting beta-carotene in half

Absorption of photon converts to metarhodopsin, which opens ion channel



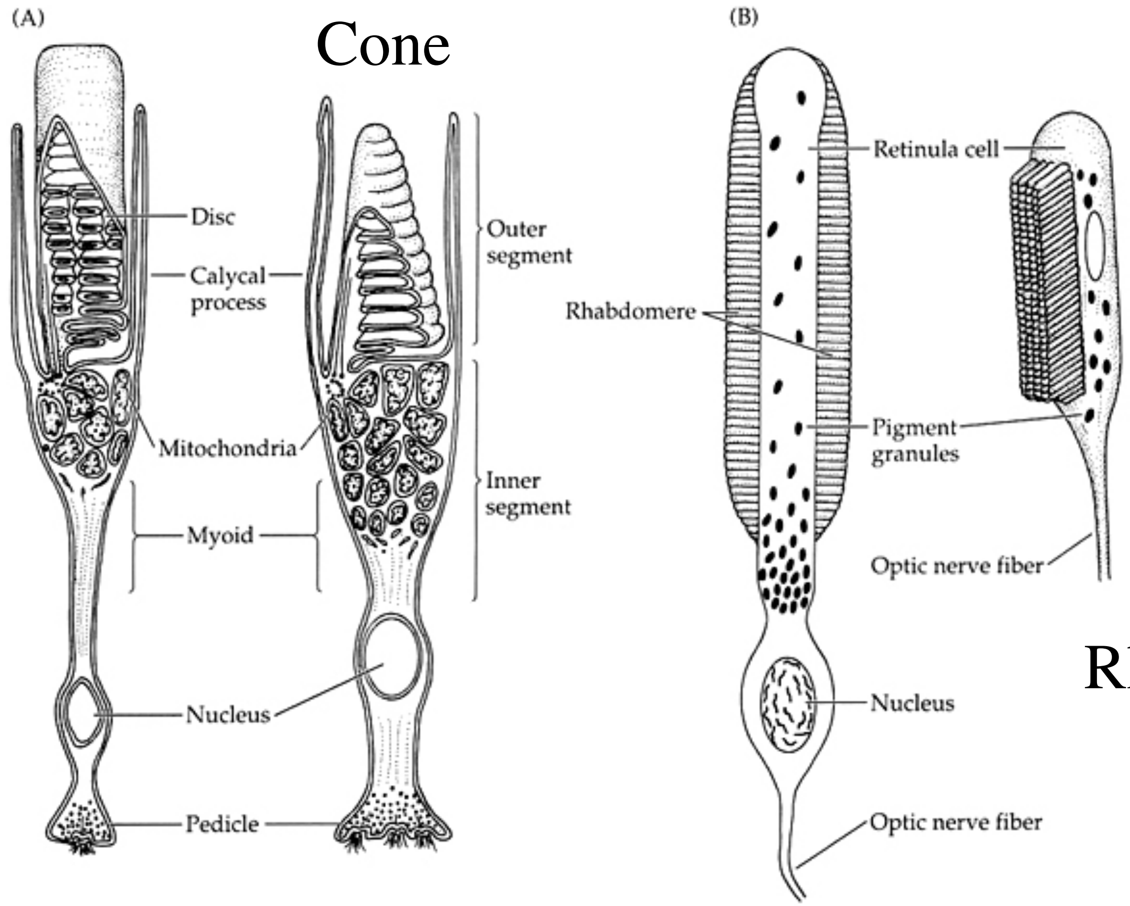


Photoreceptor evolution

Photoreceptors

Rod

Ciliary



Rhabdomeric

Figure 9.2 Structure of pigment-bearing membranes in ciliary and rhabdomeric photoreceptors. (A) Typical ciliary photoreceptors found in vertebrates (rod on left, cone on right). The outer segment houses the photopigment on invaginations of the cell membrane called discs. (B) The rhabdomeric photoreceptor typical of invertebrates anchors the photopigment on tubular extensions of the cell membrane called microtubules (octopus on left, insect on right). (A after Ali and Klyne 1985; B after Waterman 1981.)

Photoreceptor differences

Features	Ciliary	Rhabdomeric
Membranes	discs	rolls
Rhodopsin recovery	slow	fast
Pigment density	high	low

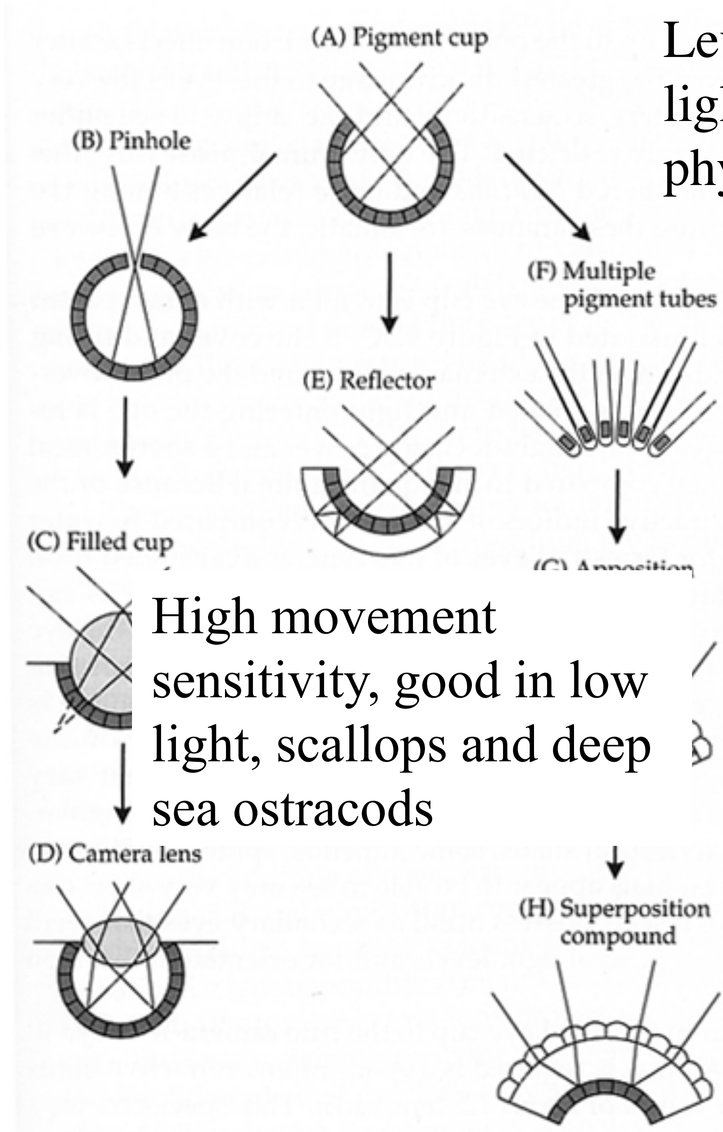
Evolution of eyes

Levels and direction of ambient light, examples in all invert phyla

Creates crude image, very poor sensitivity; Nautilus

High movement sensitivity, few annelids and starfish

More sensitive, Poor focus; ocelli of spiders



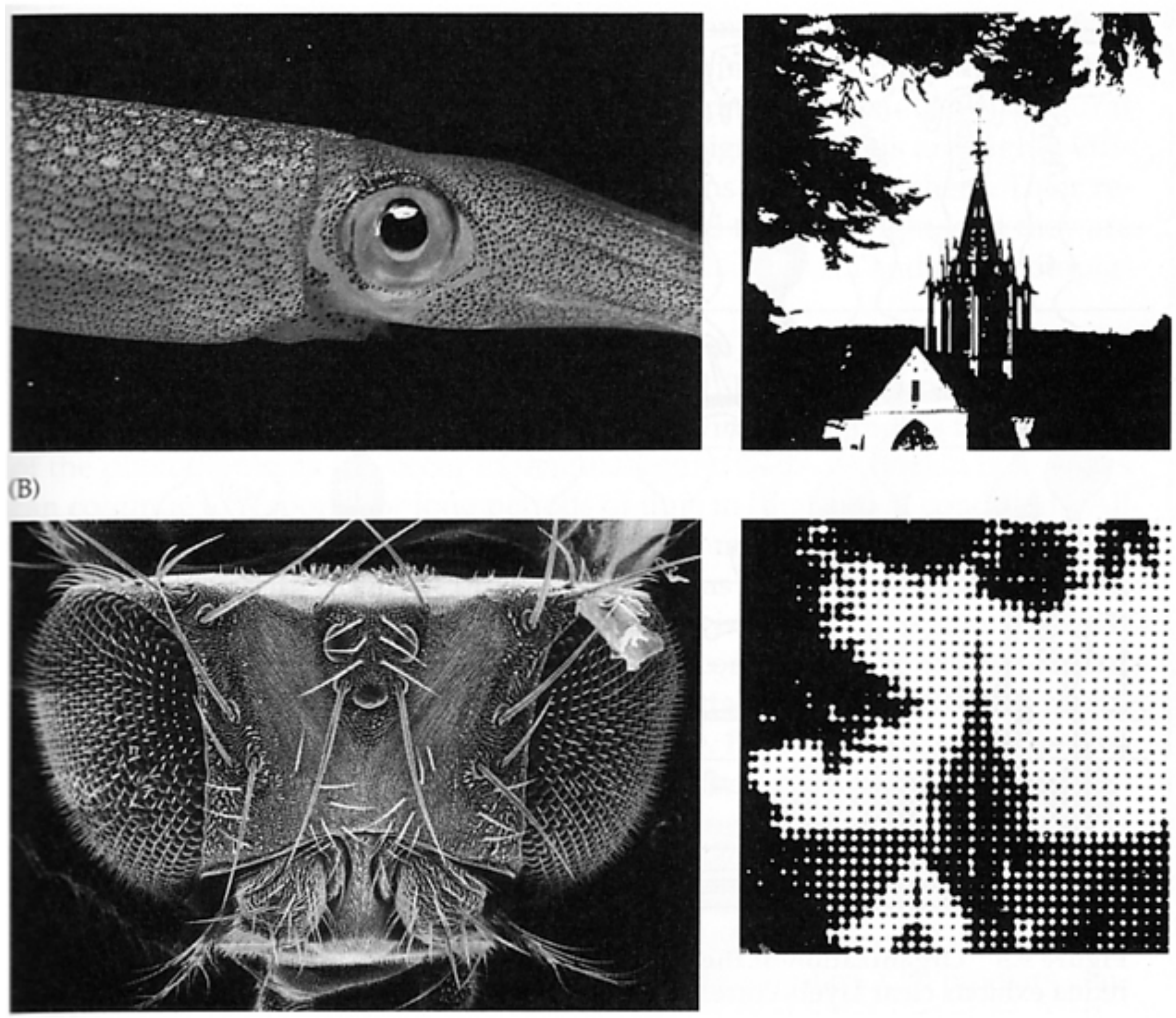
High movement sensitivity, good in low light, scallops and deep sea ostracods

Mosaic image, no need to focus, poor sensitivity in low light, lightweight; insects

Best acuity; vertebrates and cephalopods

Better in low light; nocturnal arthropods

Camera vs compound eyes



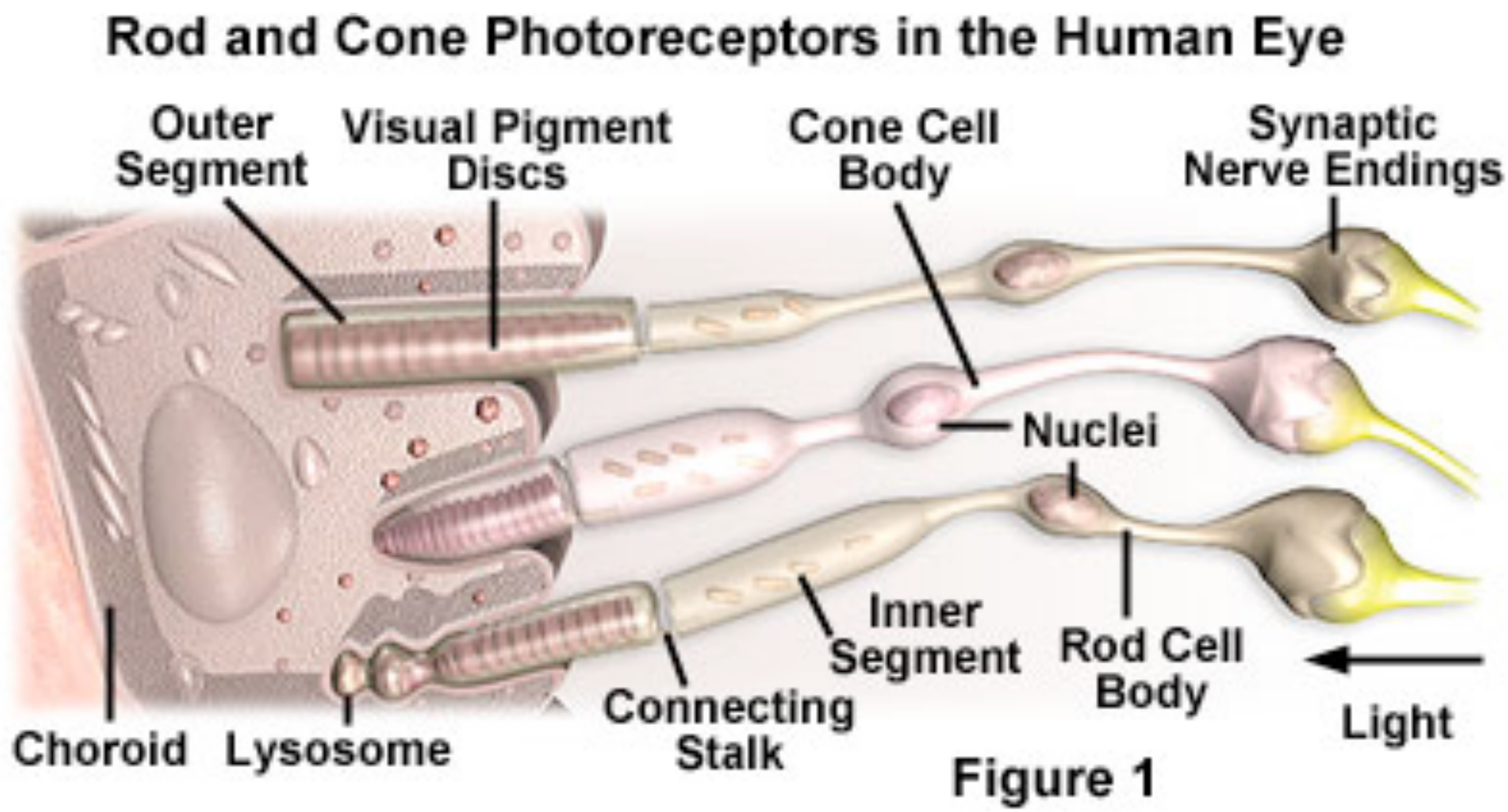
Eye number variation

Table 8-1 Number of Eyes and Receptor Cells in Various Organisms

No. of Eyes	No. of Receptor Cells per Eye	Organism	Reference
1	1	Unicellular algae	Foster and Smyth 1980
10^3	1	Volvox	Foster and Smyth 1980
2	200	Flatworm	Taliaferro 1920
1	1	Rotifer	Eakin and Westfall 1965
2	1	Certain nematodes	Burr 1984a
10^3	10	Chiton	Land 1984b
80	10,000	Scallop	Land 1984b
1	176	*Daphnia*	Macgno 1973
2+	8,500	Horseshoe crab	Land 1984a
8	10 to 10,000	Spiders	Foelix 1982, 85, 88, 92
12	~50	Ant lion	Land 1981
12	6,300	Tiger beetle	Land 1981
2+	80,000	Housefly	Shepherd 1988,,333
2	130,000,000	Humans	Levi 1980, 349

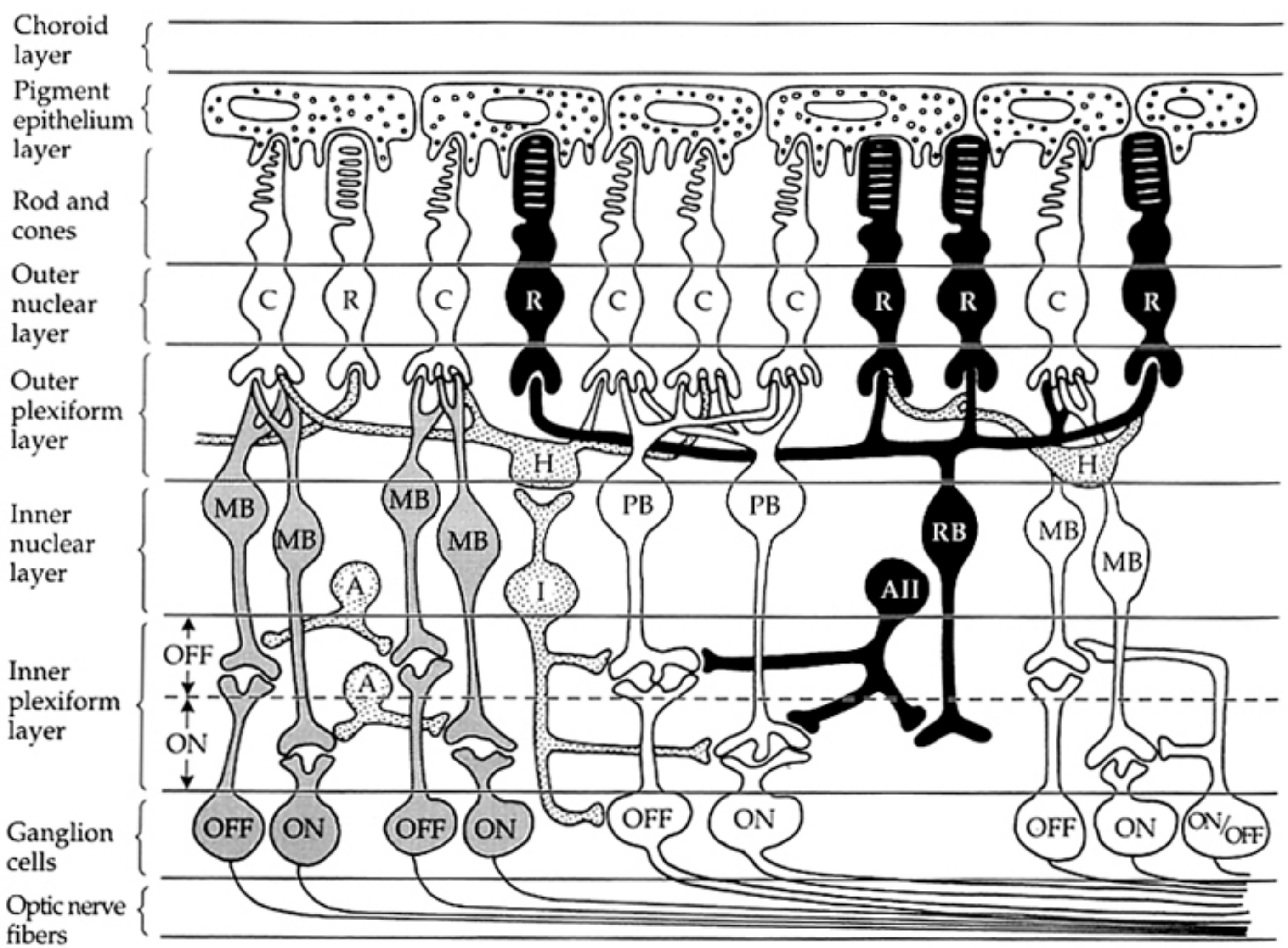
* 2+ signifies that the organism has two principal eyes, with additional much smaller eyes.

Vertebrate retina



- A reversed retina-light receptors face back of eye
- A duplex retina- contains interspersed rods and cones

Cell circuitry in the retina



R = rod (1 pigment)
C = cone (often >1 pigment, for color)
MB = midget bipolar cell
PB = parasol bipolar cell
AII = amacrine cell

10-25 rods connect to a bipolar cell

Light ↑↑↑↑

Rods vs. Cones

Rods

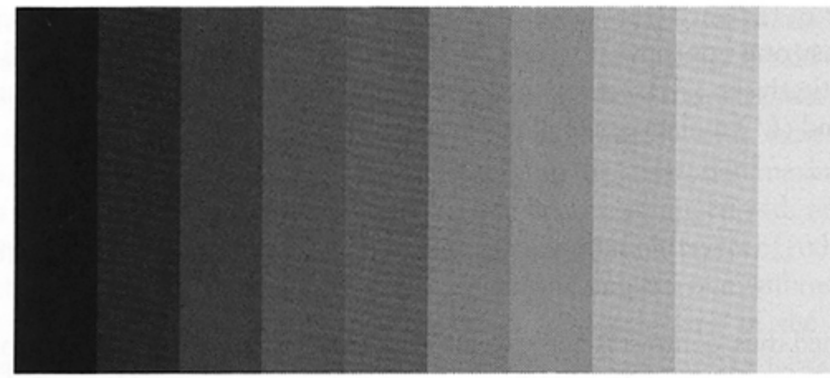
- Long, thin with internal membrane discs
- One type with single pigment
- Summation of many rods onto one bipolar cell, lots of summation of signal
- Become saturated in bright light, slow to recycle
- High sensitivity in low light

Cones

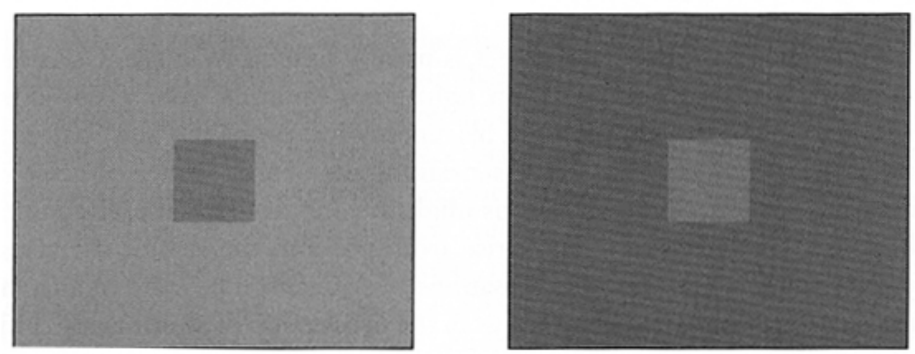
- Short, pointed with invaginated membrane discs
- Multiple types, each with a different pigment sensitive to a different wavelength
- Single cone connects to multiple bipolar cells, less summation
- Faster recycling of pigments, less saturation
- Permits color vision

Contrast enhancement

- Monochromats include
  - Nocturnal rodents
  - Nocturnal primates
  - Bats
  - Deep sea fish



- Make use of lateral inhibition for contrast enhancement



Lateral inhibition

Arrows indicate inhibition

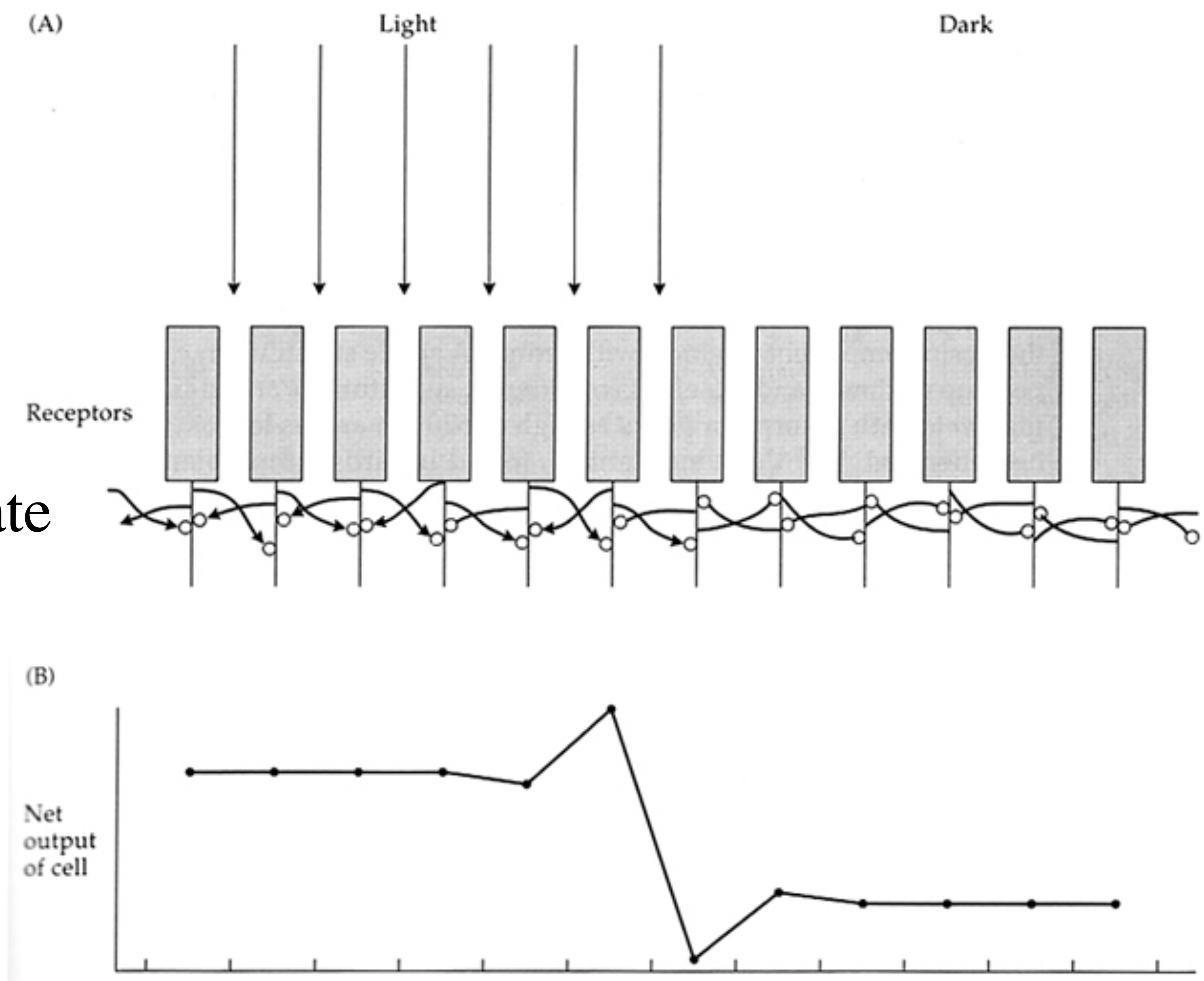


Figure 9.6 Lateral inhibition. The enhancement of boundaries in the visual field is

Mechanisms for tuning photoreceptors to colors

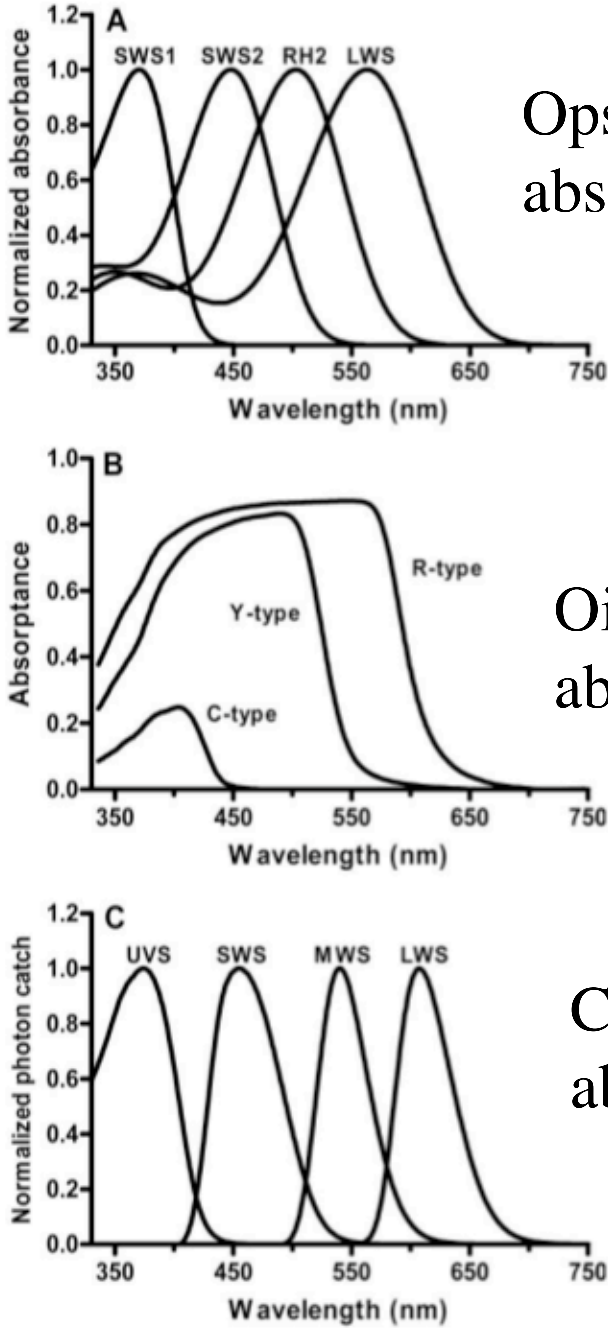
- Different variant of retinal
  - vitamin A_1 = > retinal$_1$, vitamin A_2 => retinal$_2$ shifts absorption peak 25 nm
  - Fish, some amphibians
- Change amino acid composition of opsin
  - changes absorption peak from 350-620 nm
  - Effects of single amino acid changes are predictable
  - Widespread, X-linked in primates leads to sex dimorphism in color vision
- Add colored oil droplet to the photoreceptor cell
  - Carotenoids absorb shorter wavelengths, act as filter
  - Birds, amphibians, lizards, snakes, turtles

Table 1: Site-directed mutagenesis at sites 86, 90, and 116 of ultraviolet-sensitive (UVS) and violet-sensitive (VS) pigments from different species

Pigment and mutation	λ_{max} (nm)	Reference
Goldfish UVS:		
Wild type	358	
Phe86Tyr	413	Cowing et al. 2002*b*
Phe86Val	359	Cowing et al. 2002*b*
Phe86Ser	363	Cowing et al. 2002*b*
Phe86Leu	358	Cowing et al. 2002*b*
Bovine VS:		
Wild type	435	
Tyr86Phe	363	Cowing et al. 2002*b*
Tyr86Ser	422	Cowing et al. 2002*b*
Ser90Cys	431	Fasick et al. 2002
Mouse UVS:		
Wild type	358	
Phe86Tyr	424	Fasick et al. 2002
Guinea pig VS:		
Wild type	420	
Val86Phe	367	Parry et al. 2004
Pigeon VS:		
Wild type	388/393	
Ser90Cys	359	Yokoyama et al. 2000*b*
Budgerigar UVS:		
Wild type	360	
Cys90Ser	420	Wilkie et al. 2000
Chicken VS:		
Wild type	415	
Ser90Cys	369	Yokoyama et al. 2000*b*
Zebra finch UVS:		
Wild type	359	
Cys90Ser	397	Yokoyama et al. 2000*b*

Note: For each species, the indicated amino acid substitution was made into the wild-type sequence, and the resulting opsin was expressed in mammalian cells and regenerated with 11-*cis*-retinal.

Effects of oil-droplets on color perception



Opsin absorbance

Oil drop absorbance

Cone-type absorbance

Curves show spectral tuning in the retina of the blue tit

Each photoreceptor cell has a specific oil drop filter and opsin pigment.

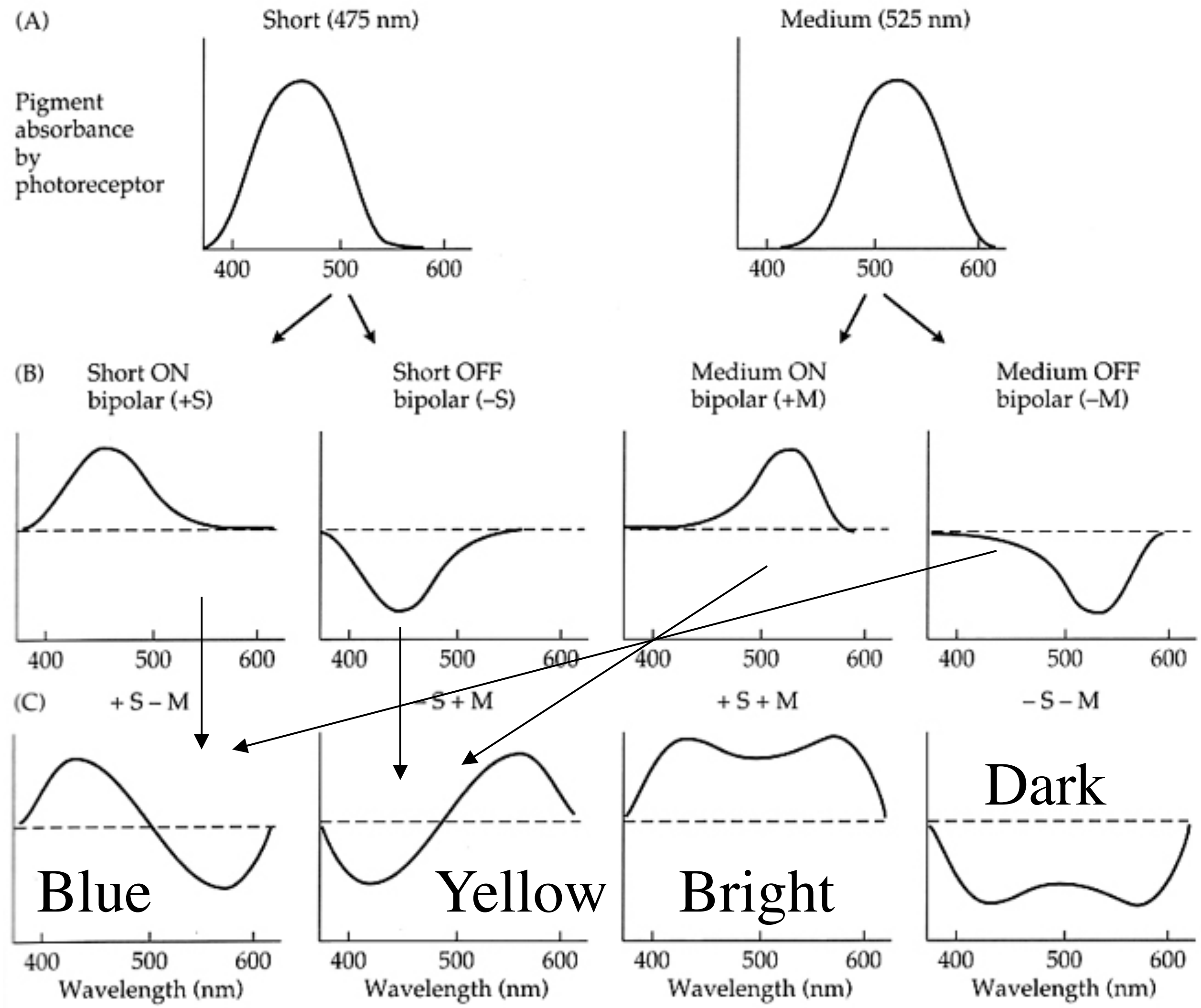
Oil drops bias sensitivity to longer wavelengths

Dichromat perception logic

Each cone cell has 1 pigment and connects to 2 bipolar cells - excitatory and inhibitory

Bipolar cells

Ganglion cells



Color-opponent cell (detect hue)

Color summation (detect brightness)

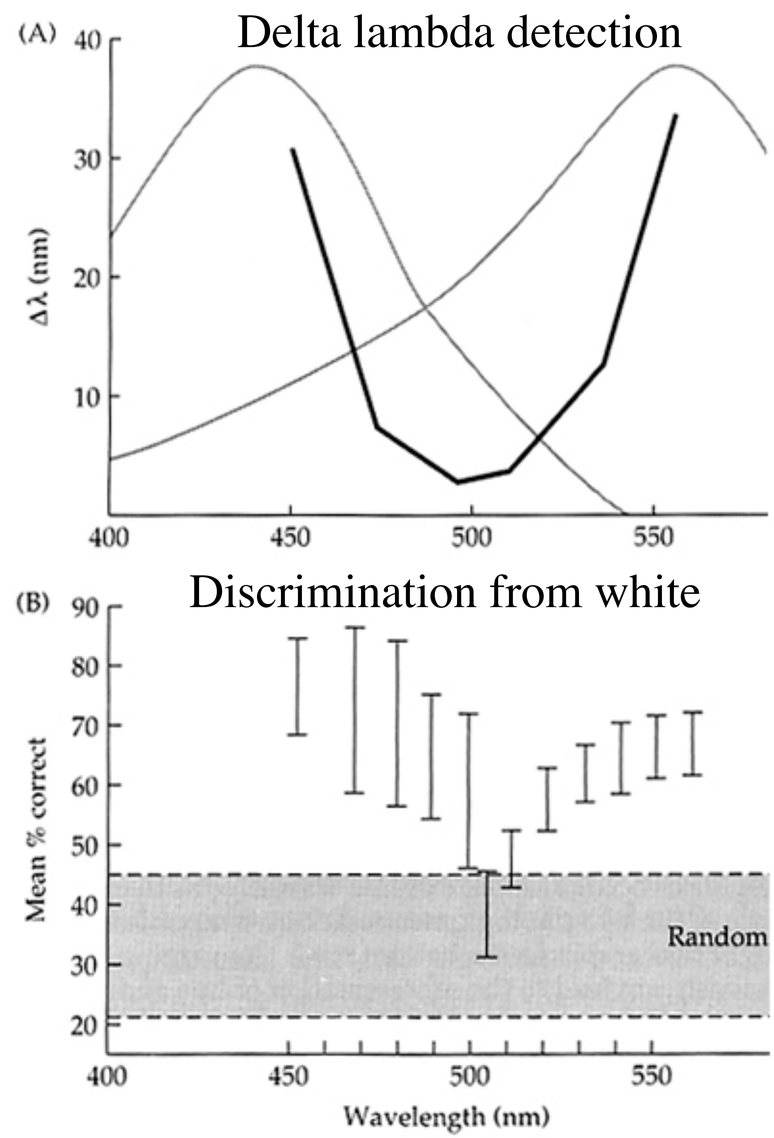
Dichromat perception

Wavelength discrimination ability and spectral peaks of two cone types. Best ability (smallest $\Delta\lambda$) is in between peaks.

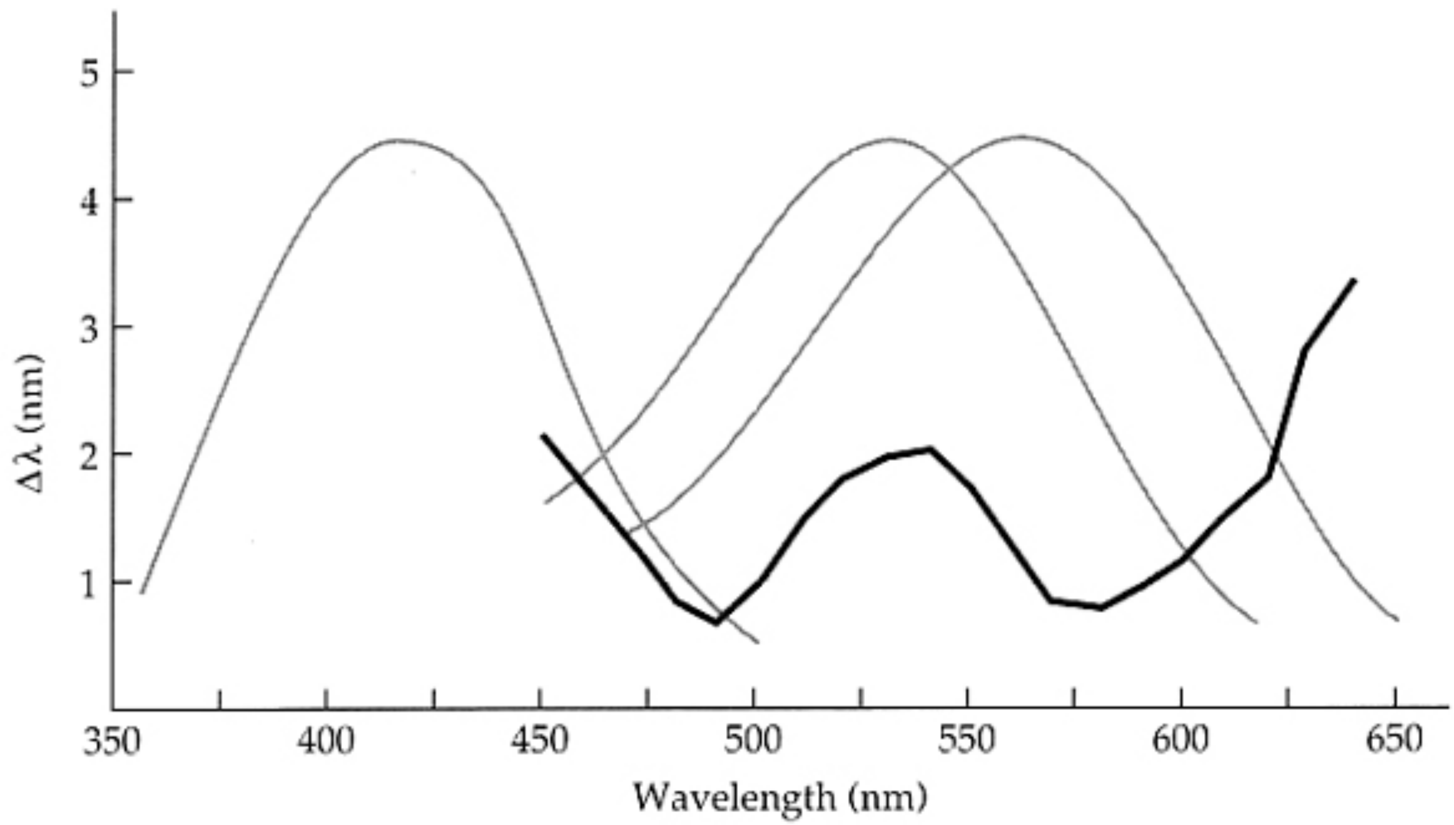
High and low wavelengths appear dark, 500 nm light (green) appears bright

Neutral point occurs where discrimination ability between white light and monochromatic light is impossible

Found in most mammals, including squirrels, cats, dogs, ungulates, New World monkeys, some fish



Trichromat perception



- Wavelength discrimination for humans, apes, Old World monkeys
- Other trichromats have different spectral peaks, include freshwater fish, diurnal reptiles and amphibians, many insect and spiders

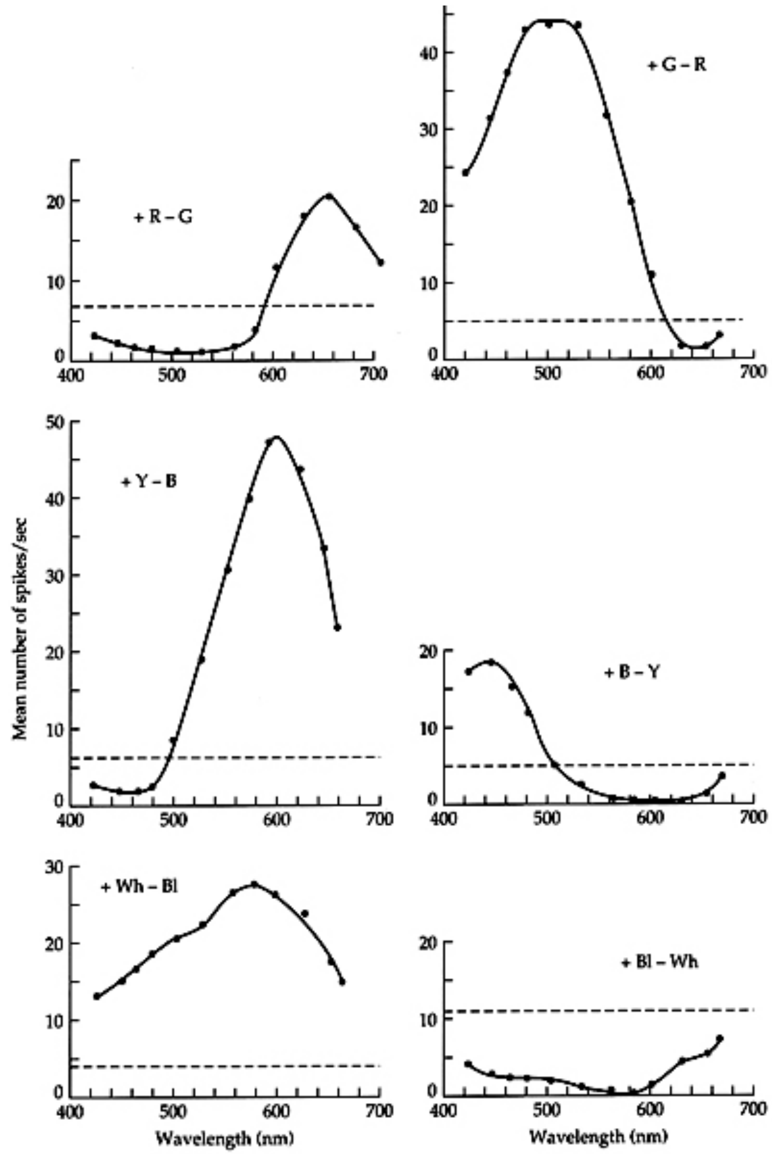
Trichromat spectral response

LGN neurons of macaque

Red-green system

Yellow-blue system

White-black system



Hue space (2D-3D-4D)

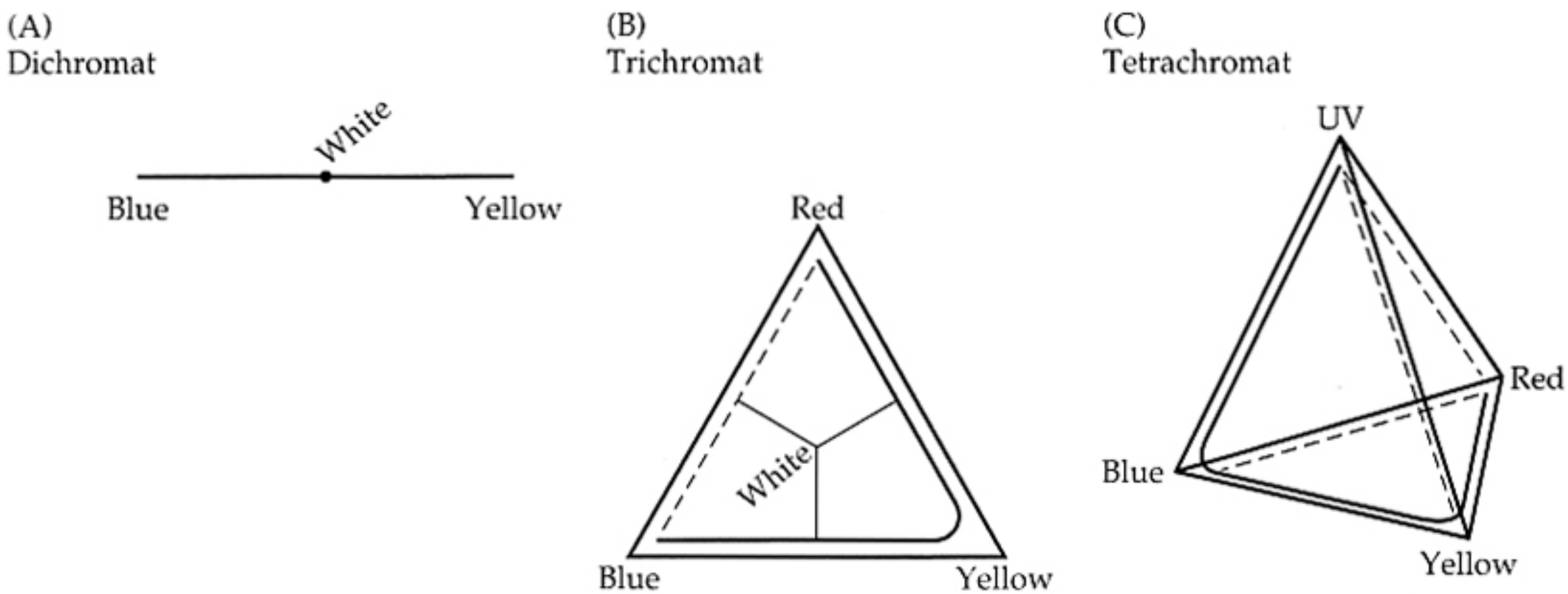
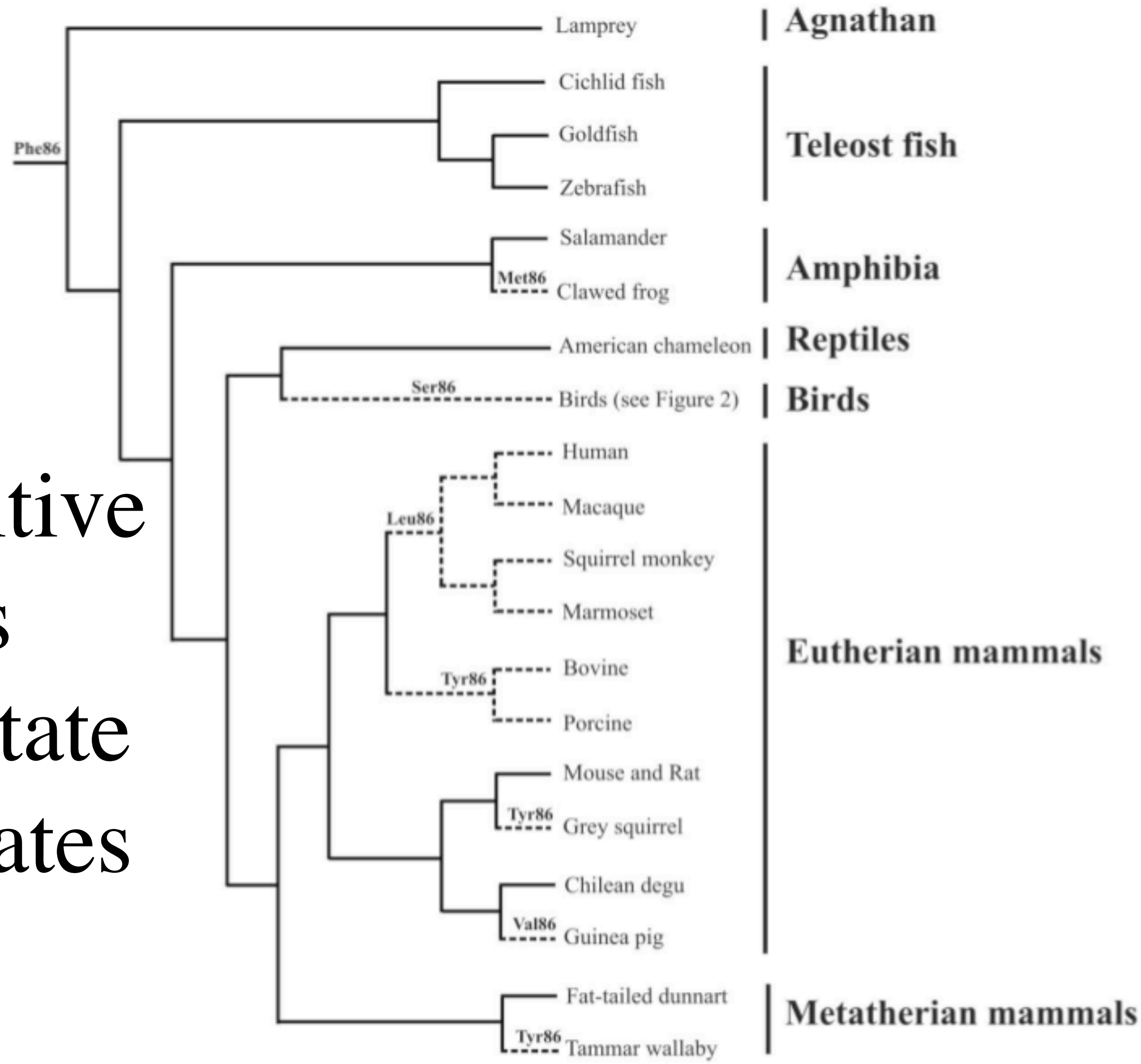


Figure 9.12 Hue space of tetrachromats compared to dichromats and trichromats. (A) The hue space of a dichromat is one-dimensional, with white occurring in the

- Some animals possess 4 or even 5 photoreceptor types
  - Often to add UV range
  - Include some birds, turtles, fish and butterflies
- Pigments may be unevenly distributed in eyes
  - Some pigments directed upward, others forward or downward

UV sensivitive opsin is ancestral state in vertebrates



Hart & Hunt 2007 Am Nat

Figure 1: Phylogeny of ultraviolet-sensitive/violet-sensitive (UVS/VS) opsins showing amino acid changes at site 86. Only where a substitution has occurred is the new residue shown on the branches. Solid lines are UVS lineages; dashed lines are VS lineages.

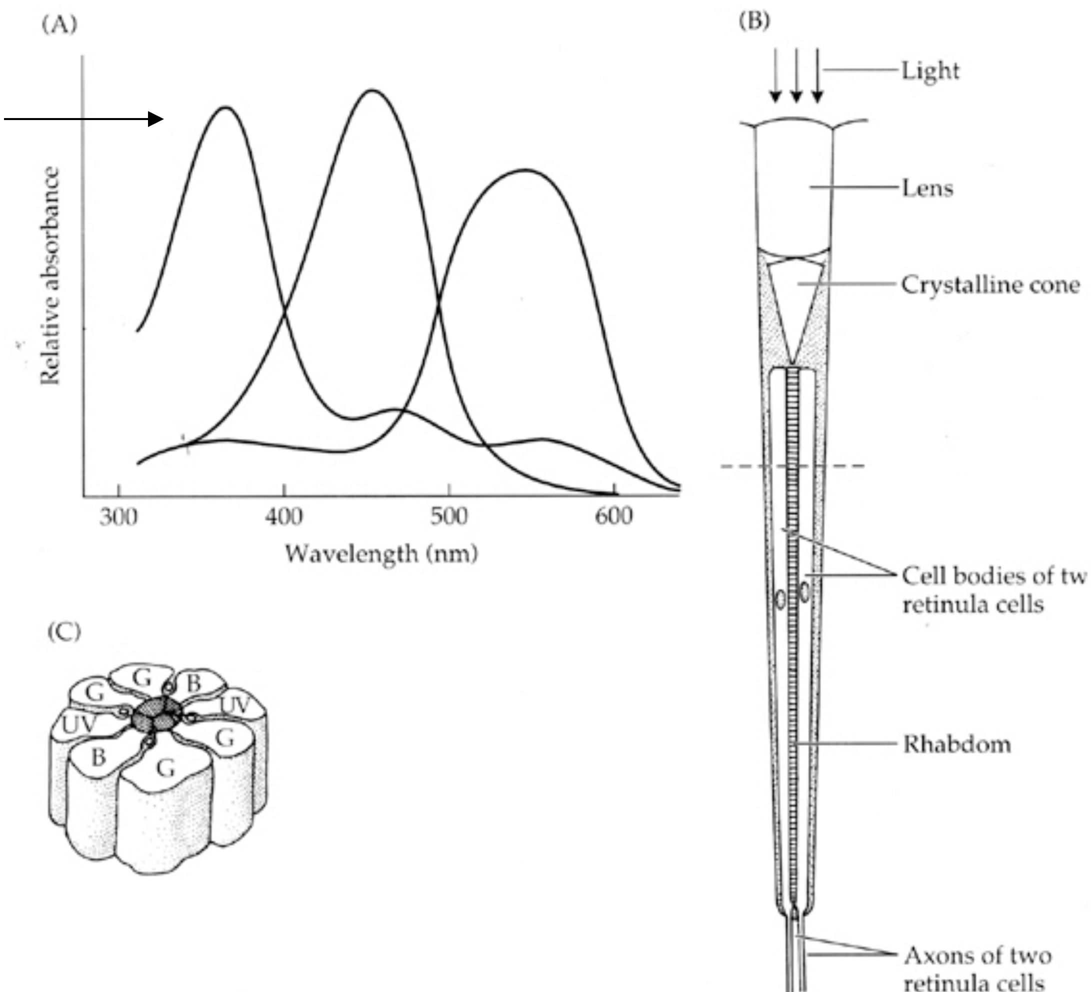
Stomatopods can have 16 photoreceptor types

Permits high spectral acuity without a complex nervous system

http://www.mbl.edu/CASSLS/thomas_cronin.htm

Bees are also trichromats

Note peak in UV →



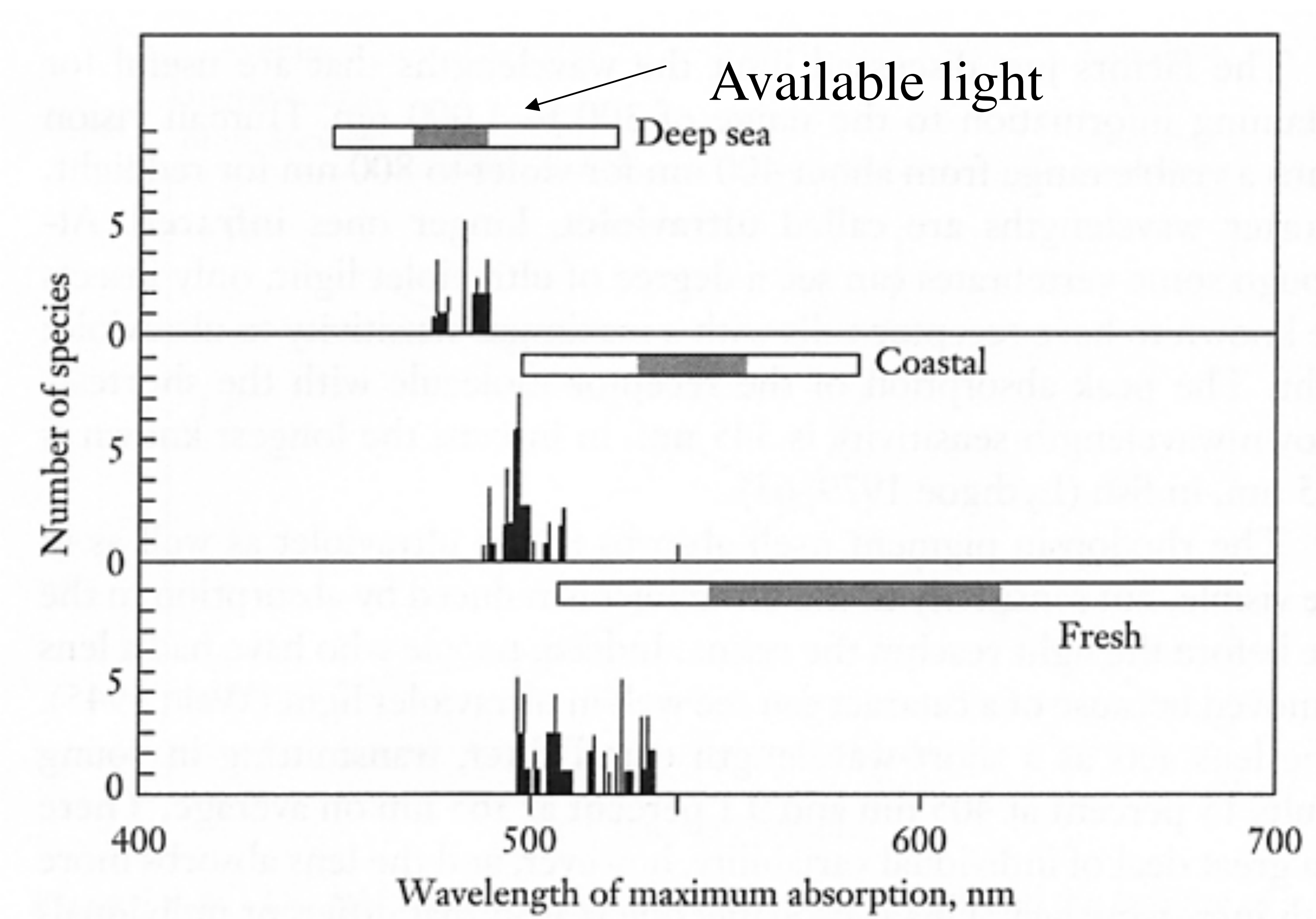
Why do bees need to see in UV?

Flowers reflect UV

Visible light image

UV light image

Pigment sensitivity in fishes



The perfect eye

- Adjustable sensitivity
- Good resolution
- Excellent accomodation (focus)
- Good spatial discrimination
- High temporal resolution (fast pigment recycling)

Optimizing sensitivity

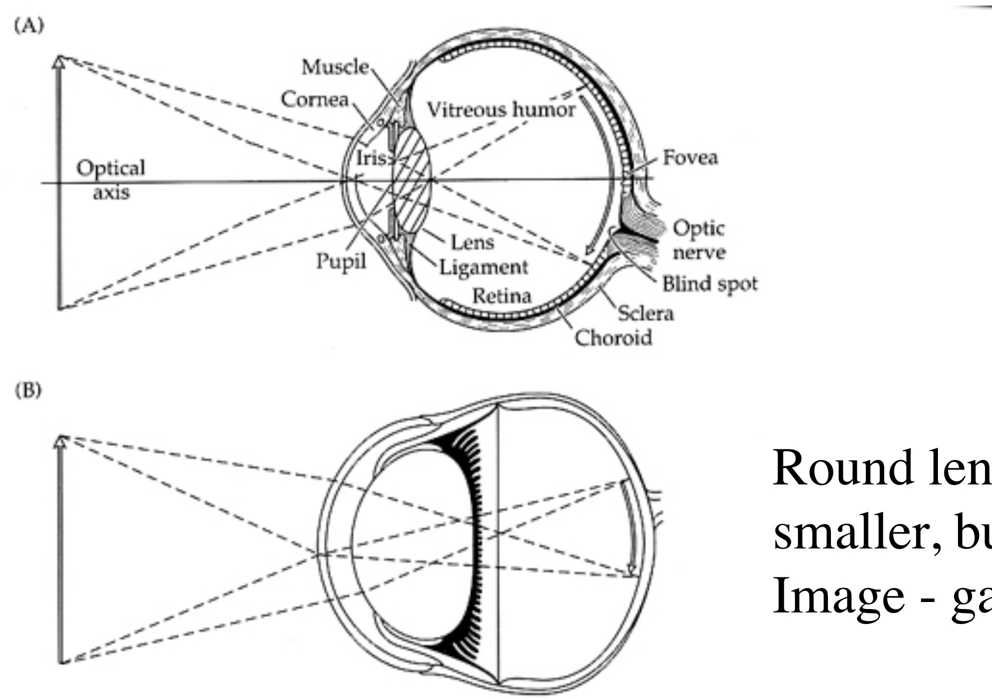
Increase sensitivity to low light

- Increase ratio of sensitive rods to cones
- Increase diameter of lens to admit more light
- Decrease focal length by increasing curvature of lens
  - Produces smaller, brighter image
- Reflective layer behind photocells-tapetum

But then need to limit bright light . . .

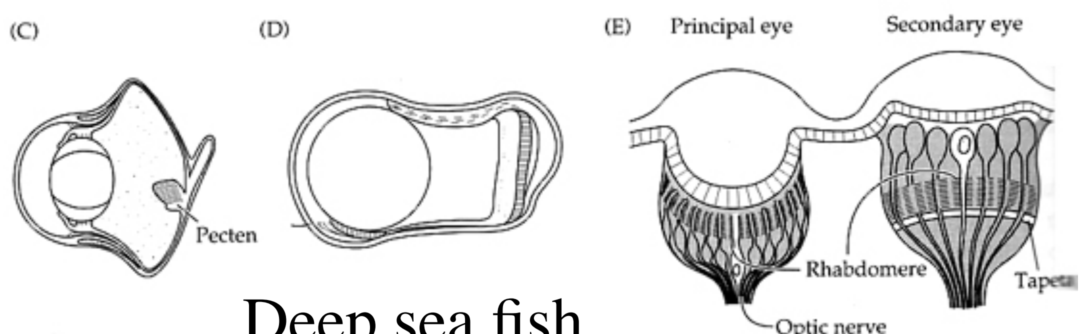
- Use round or slit pupil to limit light
- Use masking pigments to cover receptor cells

Light sensitivity and eye design



Round lens produces smaller, but brighter Image - galago

Owl



Deep sea fish

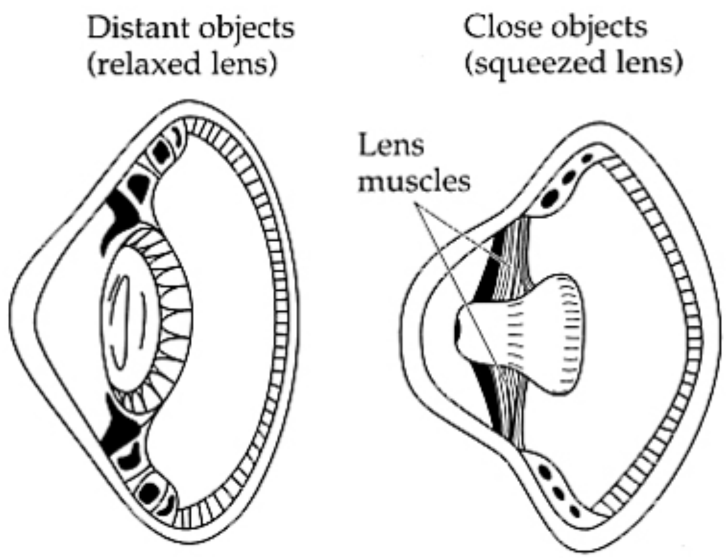
Spider - day and night - tapetum reflects

Resolution and eye design

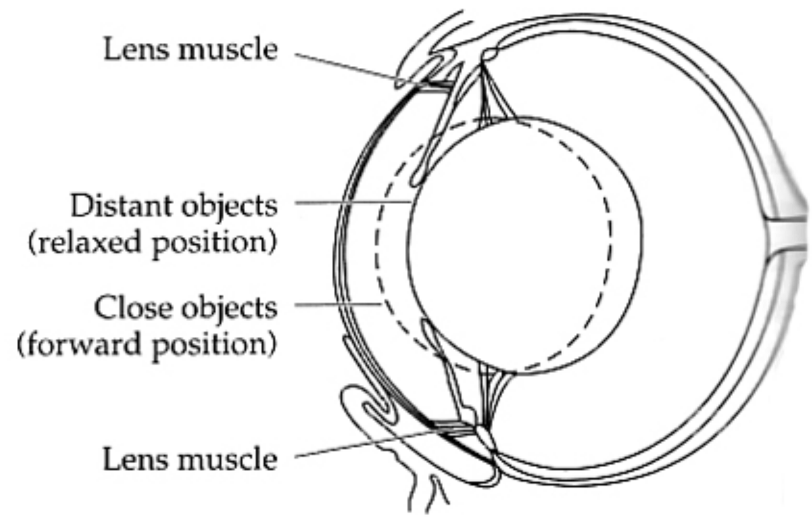
- Improve resolution of camera eye by
  - Decreasing diameter of photoreceptors
  - Increasing eye size
  - Increasing number of cones - area centralis
  - Reduce lens curvature - increase focal length, but lets in less light
- Improve resolution of apposition eye by
  - Increasing eye radius
  - Increasing facet aperture size and decreasing curvature

Optimizing accomodation

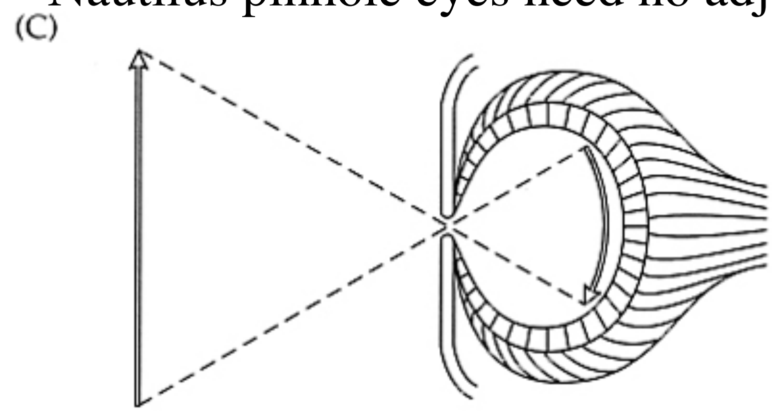
Birds and mammals adjust lens shape



Frogs adjust lens position



Nautilus pinhole eyes need no adjustment



Methods for inferring object distance

With eyes on the side of the head

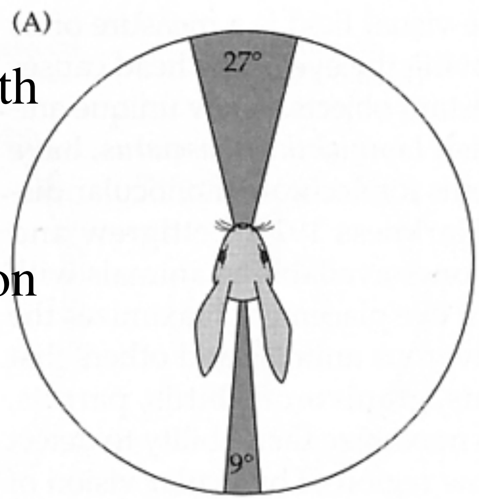
- Learn size of typical object
  - Only works with familiar objects
- Use parallax by moving head
  - Changes position of close objects relative to distant objects
- Use cues arising from accomodation

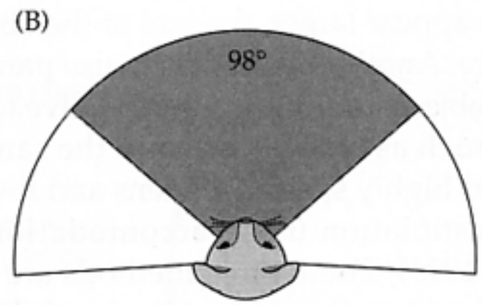
With overlapping visual fields

- Use binocular vision (angle deviation of eyes from forward position)

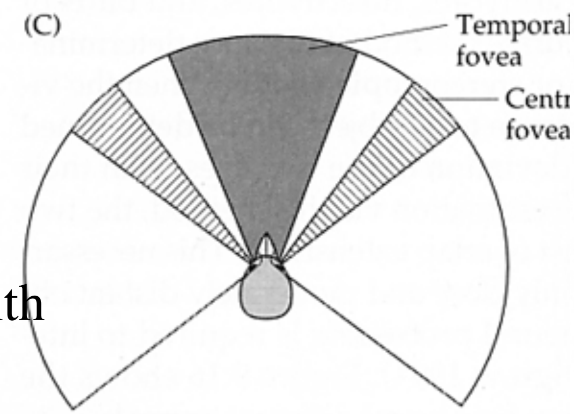
Binocular vision

Hares have both wide viewing angle and binocular vision

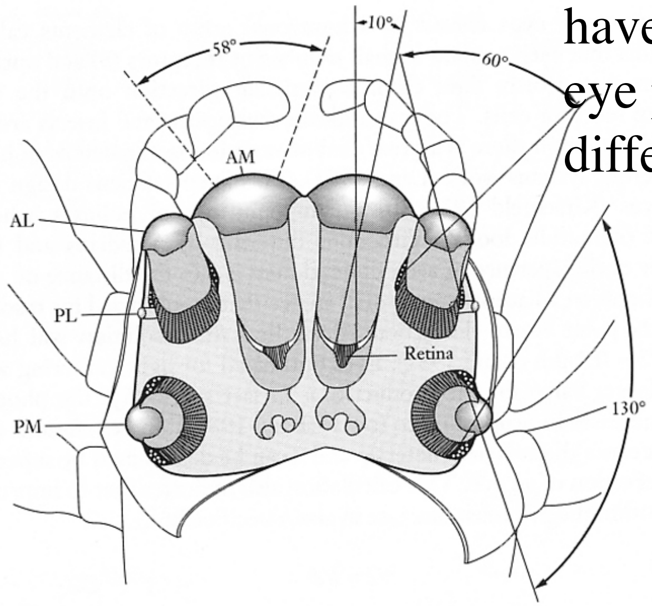




Dogs have extensive binocular field



Hawks have two fovea with enhanced resolution



Jumping spiders have multiple eye pairs with different fields

Eye resolution

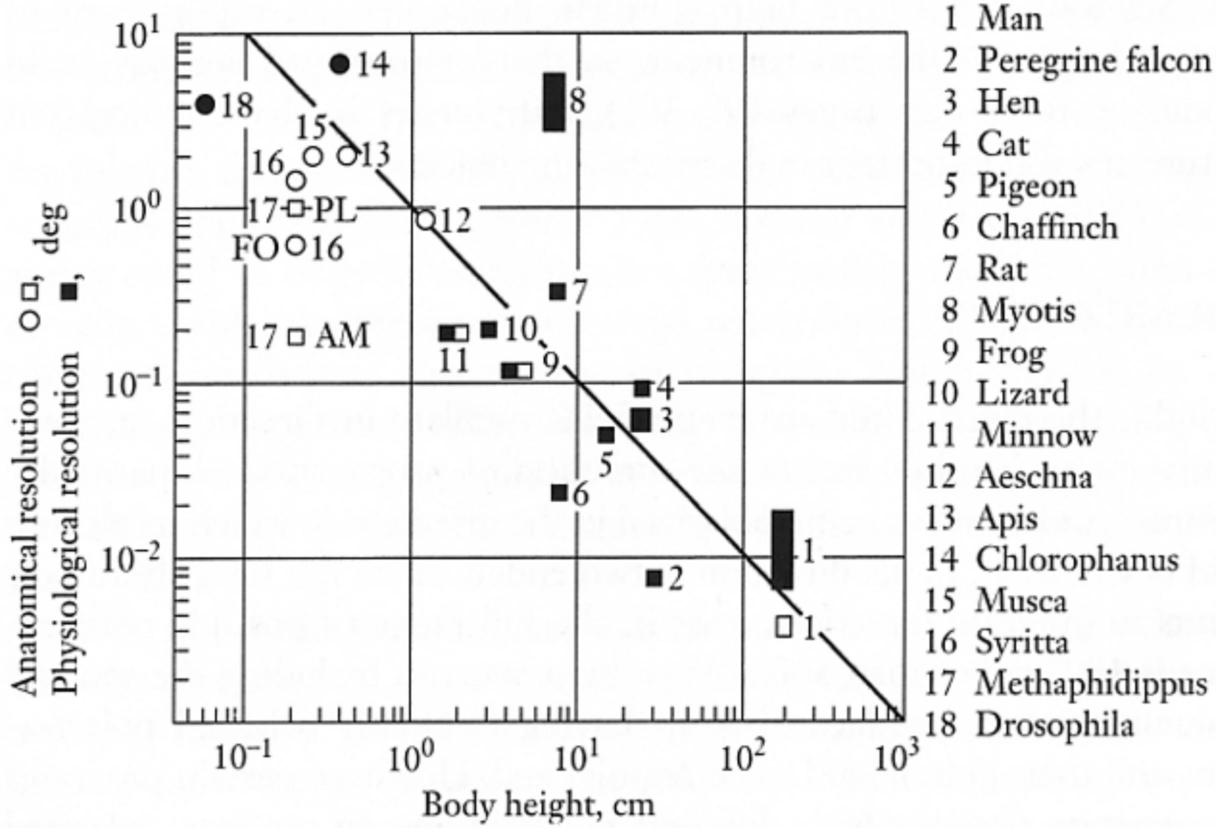


Figure 8-16 The visual resolution of eyes in various-sized animals. The body height is measured at the center of the eyes above the ground. The diagonal line represents a resolution of one degree per centimeter of body height. (After Kirschfeld 1976, 356.)

Optimizing temporal discrimination

- Temporal discrimination measured by flicker-fusion rate, the point where rapidly blinking light perceived as continuous
- Cones have higher flicker fusion rates than rods
  - Humans = 16/sec
  - all cone eyes = 100-150/sec
- Rhabdomeres have higher flicker fusion rates than ciliary photoreceptors