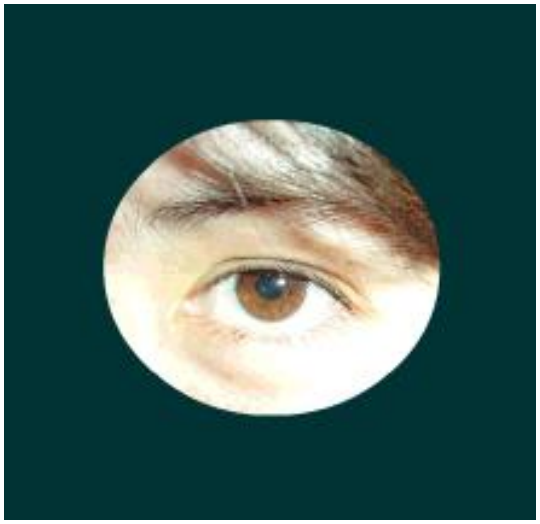
The Eye



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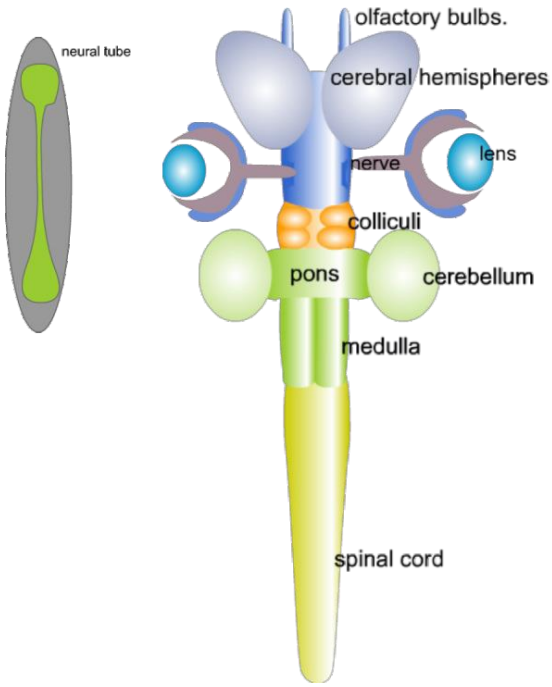
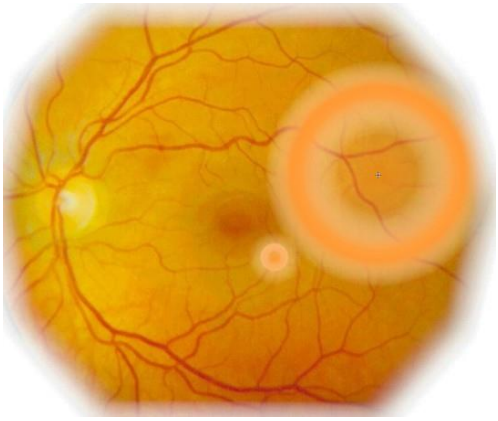


These notes on the brain begin with the eye. This is in part because the eye first develops as part of the brain. The brain begins as a sheet of cells, which when folded, becomes the neural tube. Neural stem cells divide and migrate to their appropriate layers in this tube. Forming neurons at rates up to 250,000 per minute, most of the mature brain's neurons are produced before birth. Learning precedes birth. Fetuses can learn prenatally the particular speech sounds of a mother's language.

The neural tube develops into four divisions. The most caudal division becomes the spinal cord. Next the medulla, pons, and cerebellum begin to develop. Then the superior and inferior colliculi form. The optic cups develop into the retina, the optic nerve, and the lens of the eye. The most rostral division develops into the cerebral hemispheres which in turn gives rise to the olfactory bulbs.

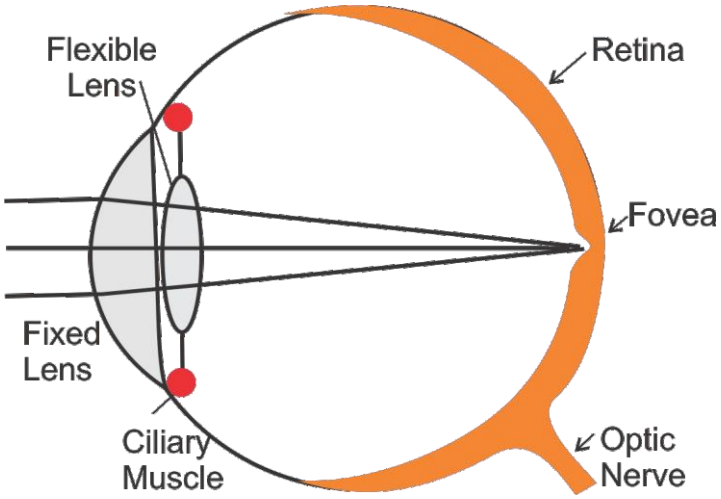
Retinal waves



The visual system also becomes highly organized before birth. This results from spontaneous waves of electrical activity that travel across the retina and down the optic nerve. These waves produce refinements in the early patterns of neural connections in the retina, the thalamus and the visual cortex.

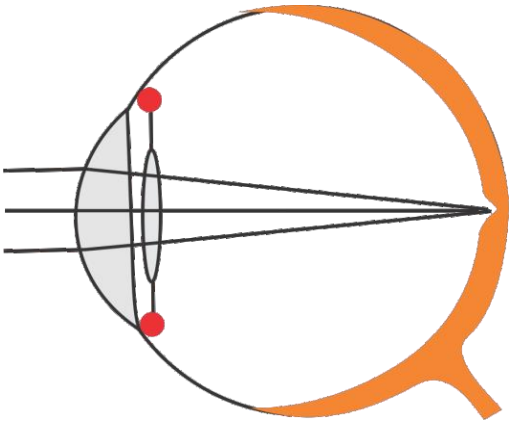
Accommodation

The lenses of the eye focus the light emitted by objects in the world onto the **retina** at the back of the eye. The retina contains light sensitive cells which convert light to electrical activity. A network of neurons collects visual information and transmits it down the **optic nerve** to the brain.

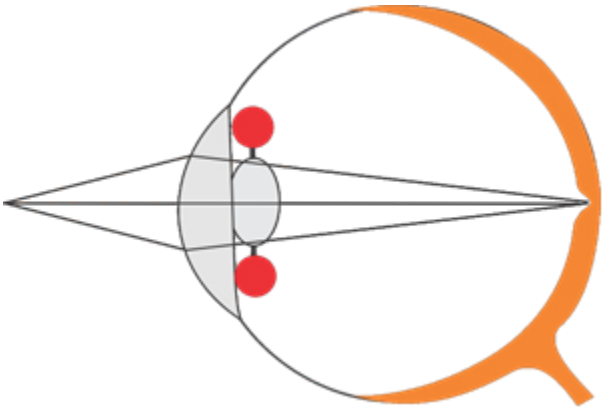


Light is focussed by two lenses: a fixed lens, **the cornea**, and a flexible lens.

The shape of the flexible lens is changed by the donut-shaped **ciliary muscles** which pull on the lens through elastic springs.



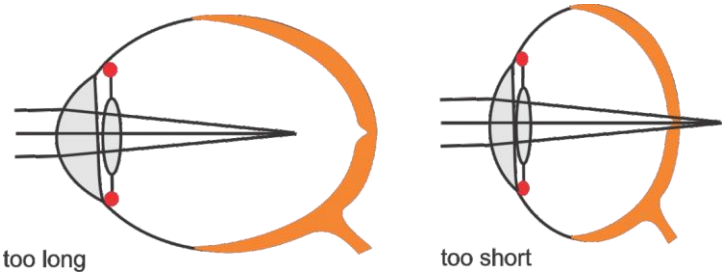
When the ciliary muscles are relaxed, the springs become tight; pulling the lens into a flat shape, and a distant object is focussed onto the retina.



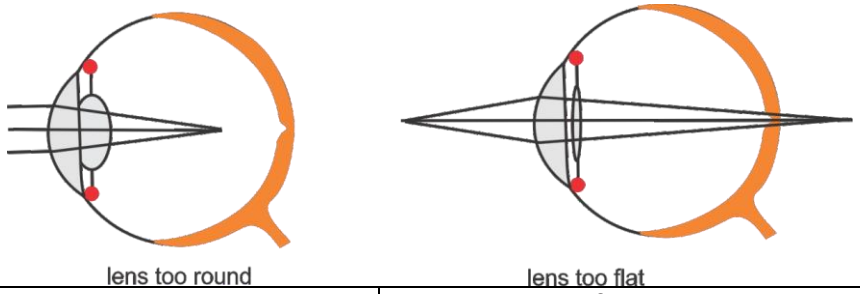
When the ciliary muscles are contracted, the springs become loose, the lens springs back to its normal round shape and a close object is focussed onto the retina.

One's ability to focus an image clearly depends on two factors.

1) The shape of the eye



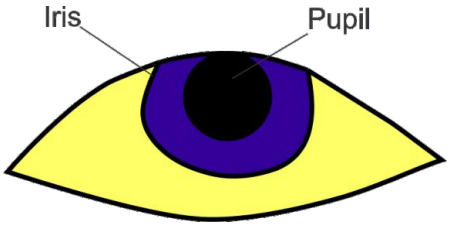
2) The shape of the lens



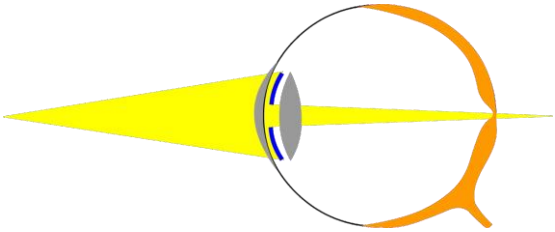
Either of the above produces eyes that cannot focus on far targets (**Myopia or near-sighted**) and need a concave lens.	Either of the above produces eyes that cannot focus on near targets (**Hyperopia or far-sighted**) and need a convex lens. 

As one gets older, the lens loses its elasticity and remains too flat even when the ciliary muscles are completely contracted.

The iris



When the lighting is bright, the iris constricts and the aperture (**the pupil**), through which light enters the eye, becomes smaller. This prevents the light sensitive rods and cones in the retina from becoming saturated by too much light.



The iris can also improve the focus of the image on the retina. Why is this? Suppose the image is not perfectly focussed on the retina. When the pupil becomes smaller in diameter, the area of blur on the retina becomes smaller. In fact if the pupil became a tiny pin hole, the lenses of the eye would become largely unnecessary.

The same thing happens in a camera when one reduces the aperture. The depth throughout which images are crisp and in focus increases.

The cell types in the retina

There are 5 types of cells in the retina:

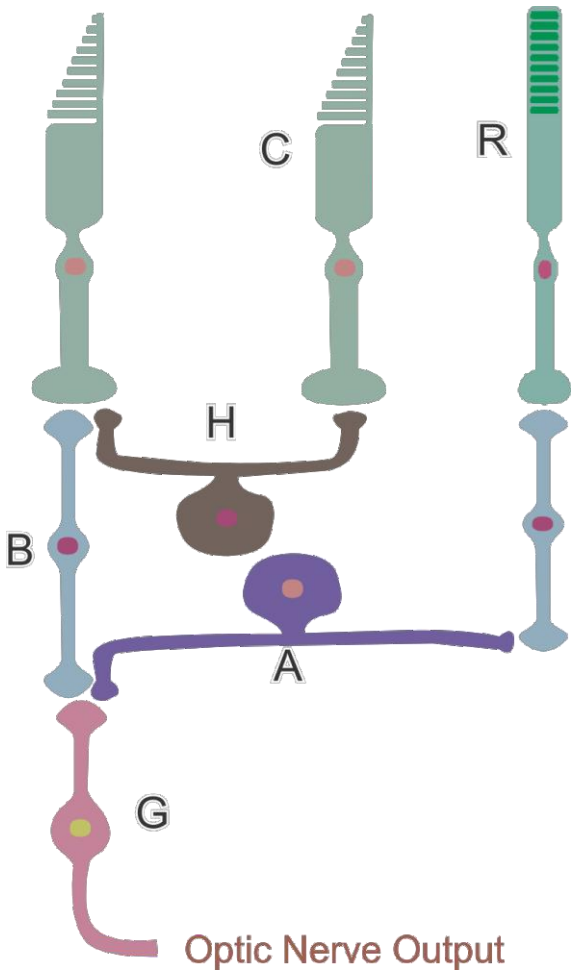
1. Light activates sensitive **receptors:**
   Cones (C) by different colors
   Rods (R) by shades of grey

2. **Ganglion (G)** cells are the only output from the eye.

3. **Bipolar (B)** cells connect the receptors to the ganglion cells.

4. **Horizontal (H)** cells converge signals from several receptors. They determine how many receptors each ganglion cell sees.

5. **Amacrine (A)** cells do the same from peripheral receptors.



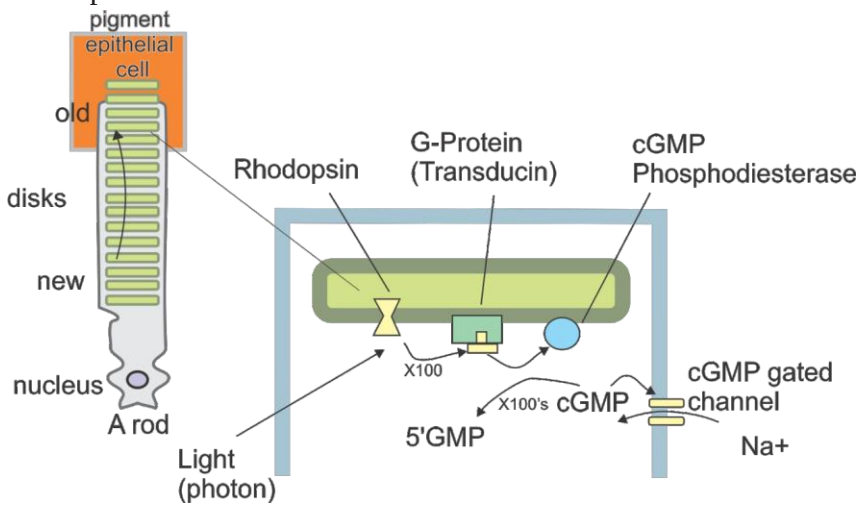
Light hyperpolarizes rods and cones (i.e. the voltage inside drops). Darkness depolarizes them (i.e. the voltage inside rises). Thus dark acts like a stimulus.

Some amacrine cells and all ganglion cells produce action potentials. Rods and cones, horizontal cells and bipolar cells only produce graded changes in potential.

Ganglion cells must transmit information over a long distance down the optic nerve. Graded changes in potential could not travel over such long distances. Thus ganglion cells must convert visual information, coded by graded potential changes in bipolar cells, into a code based on the frequency of action potentials.

How light changes the voltage inside rods and cones.

Inside rods and cones, light strikes photosensitive molecules located on disks. These disks are phagocytosed inside pigment epithelial cells and continuously replaced every 12 days.



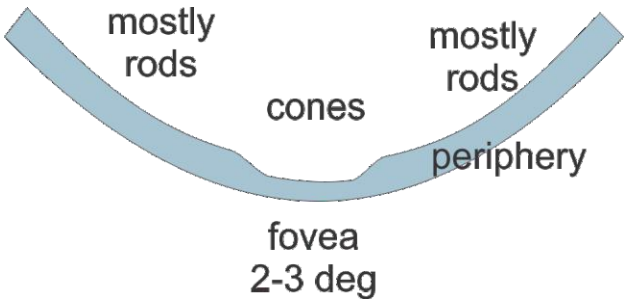
On these disks, a molecular cascade provides amplification and makes rods and cones so sensitive to light that one can see a flash from a single photon. The objective of this cascade is to control cGMP concentration.

In the dark, high cGMP concentration keeps Na+ channels open and the receptor depolarizes (becomes more +).

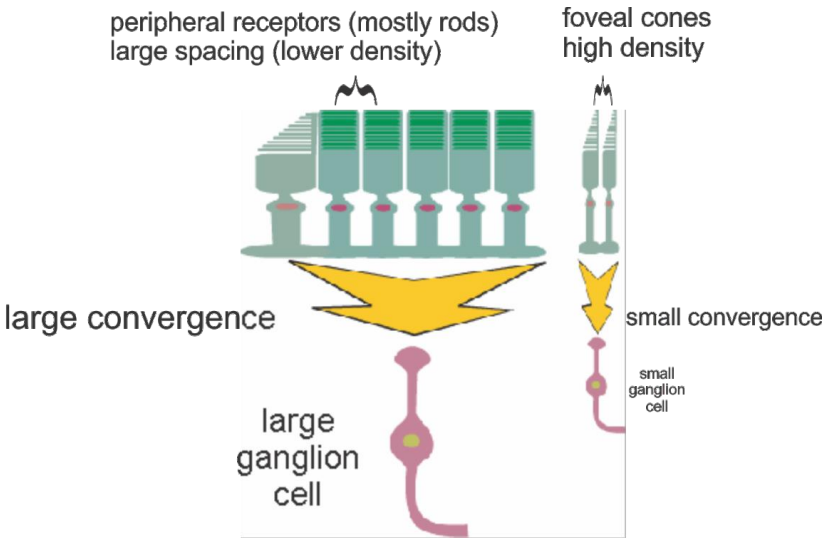
Light lowers cGMP concentration, closes Na+ channel and receptor hyperpolarizes (becomes more -). The molecular cascade amplifies the influence of a photon of light. It lowers cGMP concentration through a cascade of steps. The steps begin with one photon converting a rhodopsin molecule. The steps end in the breakdown of several thousand molecules of cGMP and the closing of several thousand Na+ channels. The cell then hyperpolarizes and less transmitter is released.

Why it is difficult to read by moonlight

The retina is not uniform. The fovea contains primarily cones. The peripheral retina contains primarily rods. Rods are more sensitive to light (can detect the faint twinkling stars).



At low levels of illumination our fovea is blind. We see with our rods and therefore see grays not colours. The rod system also has poor visual acuity (cannot be used for reading). This is because rods have a large spacing and because many rods influence a single ganglion cell (large convergence).



1. **Large ganglion cells** integrate information from a large area of retina(up to 10^0)

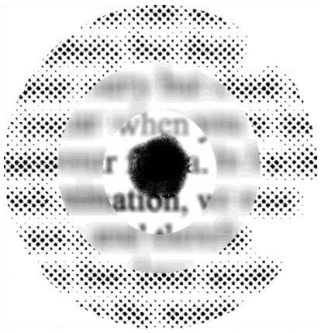
2. Large spacing and large convergence results in low acuity

1. **Small ganglion cells** integrate information from a small area of retina ($.1^0$)

2. Small spacing and low convergence results in high acuity

The retina contains a continuum of ganglion cell sizes.

What the eye sees

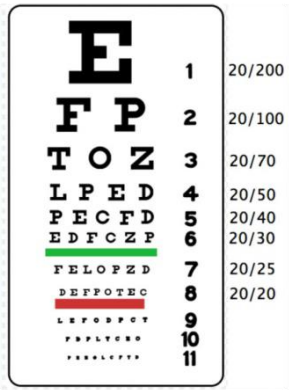
By daylight, only the central fovea sees clearly & in color.	On a dark night, only the periphery sees, only in black & white, and with poor resolution. The fovea is blind. The proper function of the rods is essential for night vision
	

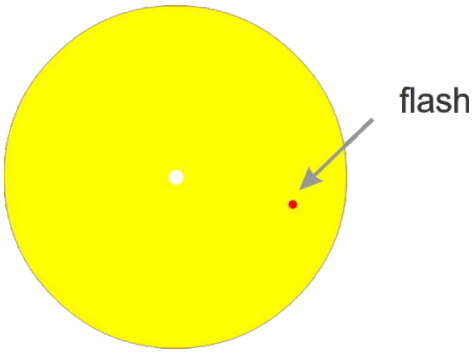
The optic nerve forms an anatomical bottleneck along the route from the eye to the brain.

This problem is solved by giving preference to foveal fibers and allowing detailed vision in only a small part of the eye.

The fovea sees only the central two degrees (1%) of the visual field: about twice the width of your thumbnail at arm's length. But the fovea takes up about 50% of optic nerve.

Tests of the fovea and peripheral



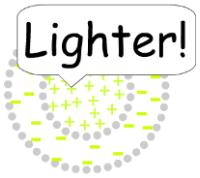


A letter chart is used to test the function of the fovea because we point it at each letter as we read.	To test the periphery, one asks patients to count fingers shown in the periphery. A Visual Field test provides a more complete picture. A small dot is flashed and the patient is asked to respond with a button press while fixating at the center. Areas of the retina that do not elicit a button press are blind spots (scotomas).

Define receptive field of a neuron

The receptive field is an important concept that applies to all the senses. The definition of the receptive field of a ganglion cell is: “That area of retina over which light stimuli change the activity of a particular ganglion cell.”

The receptive field shows which rods & cones are connected to the ganglion cell. Note! The change can be an increase or a decrease. The same definition applies to **all** other visually responsive cells. As we shall see the shape and other characteristics of the receptive field are very important in categorizing cell types and discovering their function. A similar definition applies to other sensory modalities. For the sense of touch, the skin replaces the retina and pressure replaces light.



Ganglion cells come in two flavours of antagonistic surround activity:

(a) **ON center, OFF surround** which become excited by a bright object in a dark background.

(b) **OFF center, ON surround** which become excited by the converse, a dark object in a bright background.

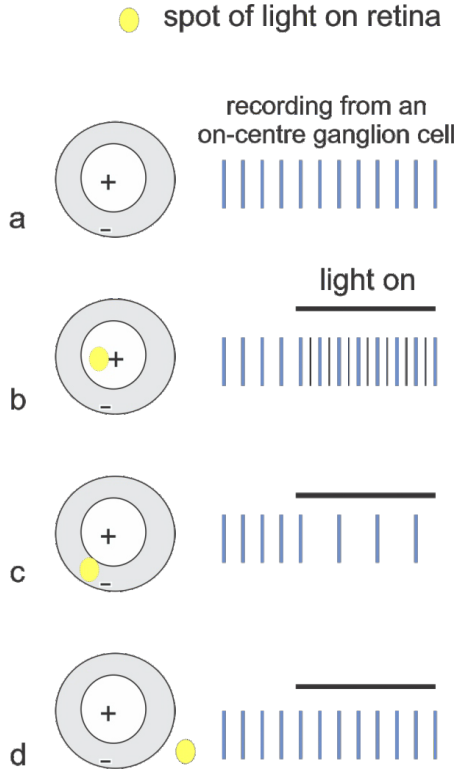
How an ON-center ganglion cell responds to a spot of light.

a) no spot, no change in tonic activity

b) spot in excitatory area, increase firing

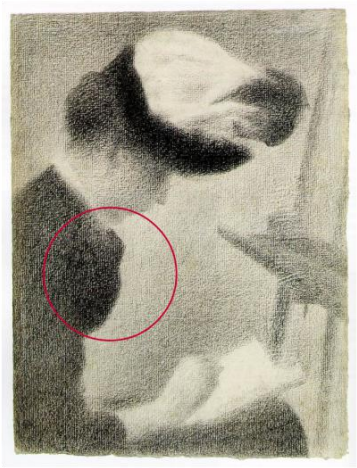
c) spot in inhibitory area, decrease firing

d) spot outside the receptive field, no change



The 1st function of antagonist surround in ganglion cells

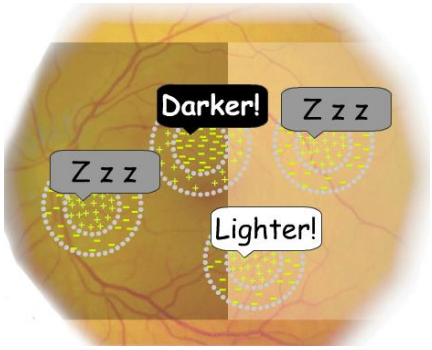
One important function of the ganglion cell's antagonist surround is to **accentuate edges**. Artists such as George Seurat in the "Woman Seated at an Easel" accentuated edges by lightening the white side and darkening the black side of an edge. The brain does the same in order to accentuate the shape and identity of objects.



When the eye sees a black white edge, the activity of ganglion cells far from the edge shows a similar low level.

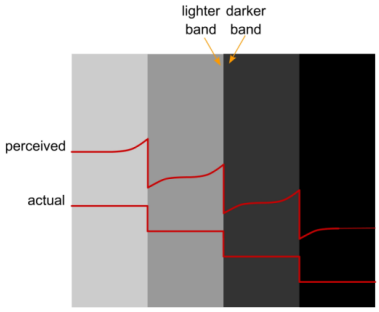
This is because both centers and surrounds cancel.

Only at the edge is the activity of ganglion cells increased.



One consequence of edge extraction by ganglion cells is the perception of illusory bands at edges.

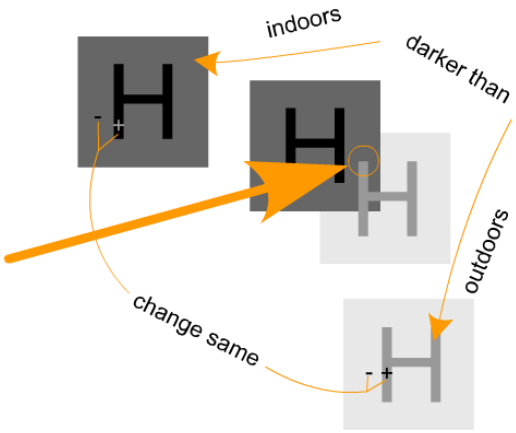
Note the darker and lighter bands. These bands are not really there.



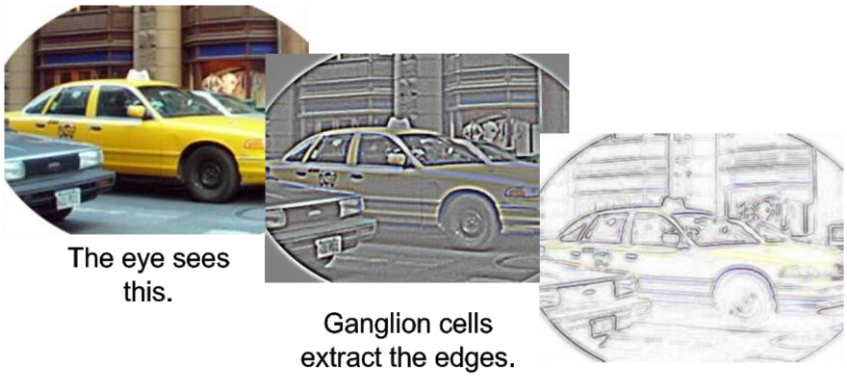
The 2nd function of antagonist surround is constancy.

Constancy allows the black letters on a page to look black whether you are indoors in dim light or outside in bright sun.

This is in spite of the fact that the white paper indoors reflects less light (is more black) than the black letters outdoors. Ganglion cells provide constancy by measuring only the **change** across an edge. The increase or decrease of light coming from the whole page is largely ignored.



In summary: vision involves extracting key features



The eye sees this.

Ganglion cells extract the edges.

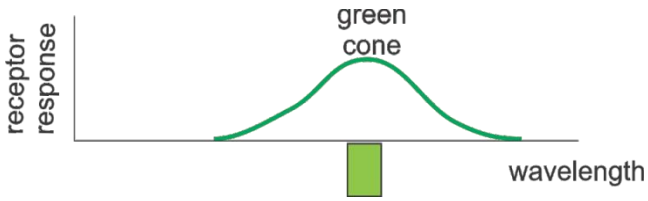
In the next session we will see how some cells in the visual cortex extract lines and corners.

Colour vision

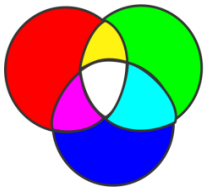
Which tastes better?

Color helps us choose food that is edible.

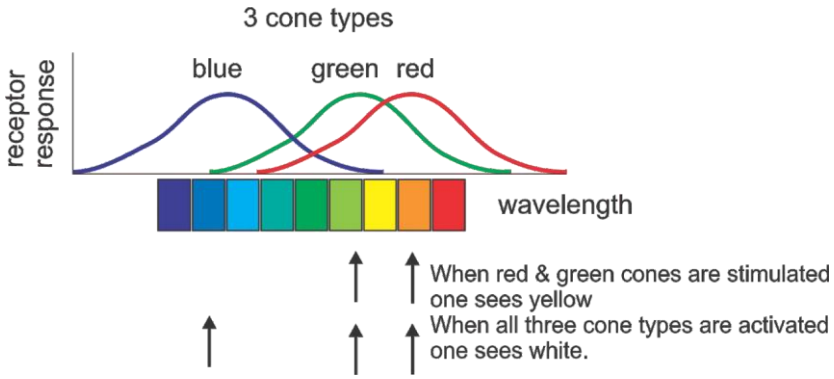
Cones respond best to some wavelengths of light and less to others.



This one responds better to various shades of green light. We have three cone types.



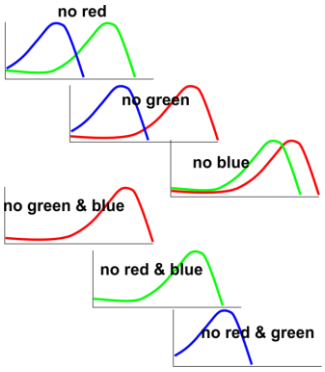
The effect of mixing different wavelengths of light



Colour blindness

Each cone type contains a different light sensitive photo molecule. Colour blindness occurs when there is an inherited, sex-linked defect in the genes that produces these molecules. Some of defects that can occur are shown here. One can be missing 1 cone type, 2 types or all 3 (not shown). When all three cone types are missing

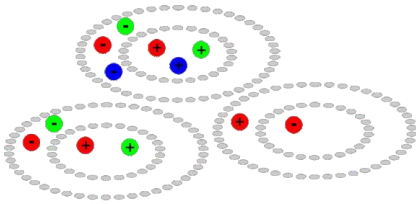
- vision is limited to the rods and
- the patient has only peripheral, not foveal, vision.



Cells that receive input from cones

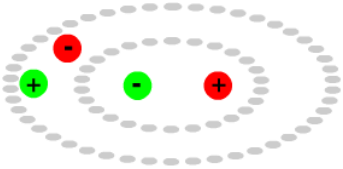
Ganglion cells that receive input from cones come in a variety of flavors. Shown here are three. What properties do they all share?

1) The center and surround contain the same combination of cone types.
2) The influence of the center is the opposite of the surround.



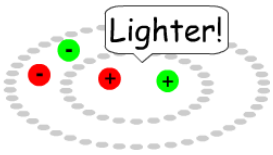
Ganglion cell

This makes these cells good at detecting a change in the **brightness**. Surprisingly like cones, they are not very sensitive to a small change in color. How does one make a cell that is sensitive to a small change in color?

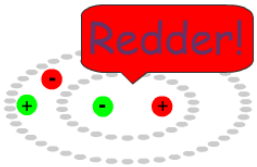


double opponent

Double opponent cells are sensitive to small changes in color. This cell type is not found in the eye but in the "blobs" of the visual cerebral cortex. This double opponent cell is sensitive to differences in red. One also finds blue - yellow double opponent cells.



What is the advantage of the double opponent type? This type is more selective for a particular color. Consider the effect of a spot of yellow light. Recall the yellow light is the combination of red and green light. The ganglion cell will respond not only to pure red but also to yellow. This double opponent cell will not respond to yellow, only to shades of red.



Why does a green object against a red background stand out so well?

A red spot in the centre activates the double opponent cell shown above. A green spot in the surround also activates the cell. A red fruit against a green gives the maximum response. This is why complimentary colours stand out.

What happens when you shine diffuse red light over the whole receptive field?

Diffuse red light over the centre and the surround produces cancellation. Diffuse green light does the same, as does any diffuse colour. Because the centre and surround produce opposite responses, such a cell is unaffected by any background colour (e.g. diffuse yellow light over the centre and the surround) and thus maintains colour constancy.

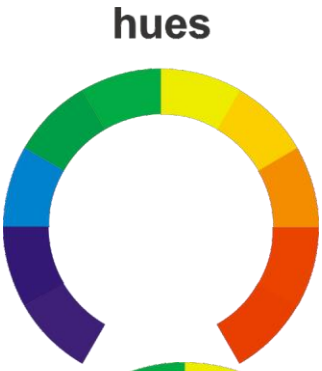
What happens when you use an outdoor setting to take indoor pictures?

Your pictures will have a yellow hue from the background incandescent lights. Cameras measure absolute colour and do not have colour constancy.

How many gradations of colour can the human brain distinguish?

a) 200 **hues**

The brain transforms the single wavelengths of light seen in rainbow into a colour circle. Hues on opposite sides of the circle are complementary.



b) 20 levels of **saturation**

Saturation is the combination of two complimentary wavelengths. When complementary wavelengths are combined equally, one gets white.

c) 500 **brightness** levels

Any colour on the circle can be made brighter or darker. But because very bright or very dark colors are more difficult to distinguish, the circle becomes narrower.

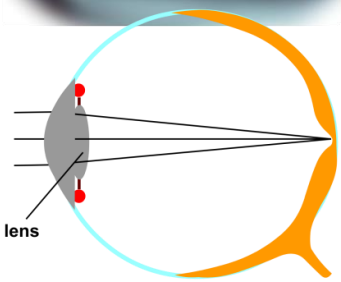
Remarkably with only 3 cones types we can see 500x200x20 = 2,000,000 gradations of color

Three diseases of the eye

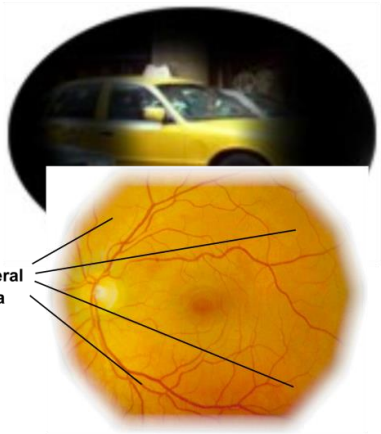
Cataract

Vision becomes **dull and blurry**.

The lens becomes cloudy because the proteins of the lens begin to clump together.



Glaucoma



The first to be affected is **peripheral vision**. Patients feel that they are looking through a tunnel

Increased pressure inside the eye compresses the axons of ganglion cells. These axons form the optic nerve. The large ganglion cells from the peripheral retina are most susceptible to increased pressure.

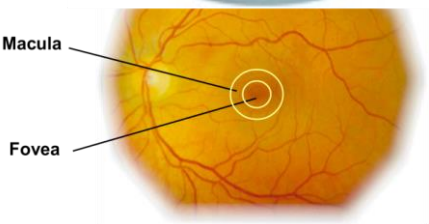
Macular degeneration

This is a disease that affects **central vision** and is the most common cause of vision loss in people over the age of 55.

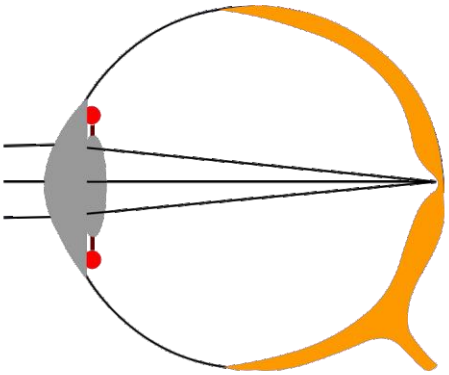
It is caused by break down of the light sensitive cells in the macula or by new blood vessels behind the retina growing toward the macula.

The macula is the central part of eye that includes the fovea and is normally relatively free of blood vessels.

The growth of blood vessels causes a distortion of the retinal sheet which in turn distorts the image.



In summary



The eye does three things.

1) It focuses the image clearly on the retina.
2) It detects light of various colours and intensity.
3) It compresses the information in order to send it down the small optic nerve.

Compression occurs in two ways:

1) A detailed image is sent only from a small part of the eye, the fovea.
2) Only the changes in colour or brightness, the edges, are transmitted.

It would seem that what is sent to the brain is a poor reflection of the original image. Yet we perceive the world around us in extreme clarity. How this is done, and surprisingly how the brain improves on what the eye sees, is the subject of the next chapter.

Practice problems

1. It is difficult to read by moonlight because
a) the rod system has poor visual acuity.
b) the cone system has poor visual acuity.
c) the cone system is very sensitive to low levels of light.
d) the rods are more closely spaced than are the cones.
e) at low levels of illumination we see only with our fovea.

2. When rods are subjected to darkness
a) the electrical potential inside the cell decreases.
b) the concentration of cyclic GMP increases.
c) Na+ channels close.
d) more rhodopsin is broken down.
e) none of the above.

3. Presbyopia (difficulty focusing at near due to ageing changes in the eye) results from decreased ability of the
a) cornea to alter focusing power.
b) pupil to constrict.
c) lens to spring back to its round shape.
d) lens to spring back to its flat shape.
e) ciliary muscles to constrict.

Answers

1. a)
2. b)
3. c)

Also see http://www.tutis.ca/NeuroMD /L1Eye/EyeProb.swf