

The Physiology of the Senses

Lecture 1 - The Eye

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Objectives

1. List the factors that prevent an image from being clearly focused on the back of the retina.
2. Identify how all of the information that is sensed by a relatively large retina can be funnelled down a relatively small optic nerve.
3. Specify the transformations that are performed by the neural circuits within the retina.
4. Specify why the receptors in the retina are not adequate for distinguishing colors.

Introduction

This course attempts to emphasize the “why's”. Why your brain is built one way and not some other way?

One example: The cost of a single action potential is high. If we activate much more than 1 or 2 % of our neurons at the same time, we run the risk of fainting from a depletion of the brain's oxygen.

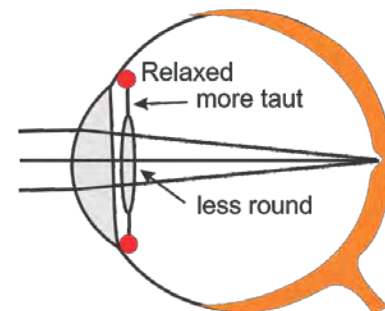
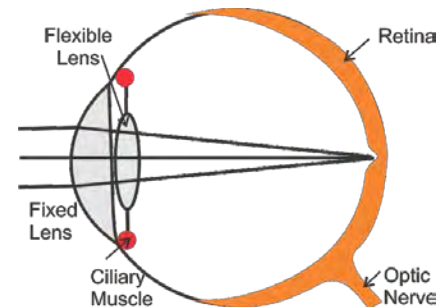
Question 1: How does the brain compute so much using so few active neurons?

But before we can attempt to answer these questions, we first need to appreciate our brain's basic building blocks. Today we will look at some of the key building blocks in your eye.

1. The lenses of the eye focus the light emitted by objects in the world onto the retina at the back of the eye.

2. The **retina** contains light sensitive cells which convert light to electrical activity.

3. A network of neurons collect visual information and transmits it down the **optic nerve** to the brain.

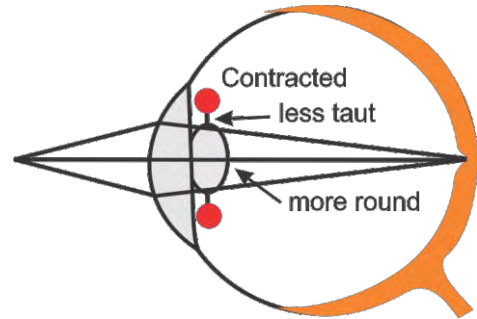


Accommodation

Light is focussed by the curvature of two lenses: a fixed lens and a flexible lens.

The curvature of the flexible lens is changed by the donut-shaped **ciliary muscles**.

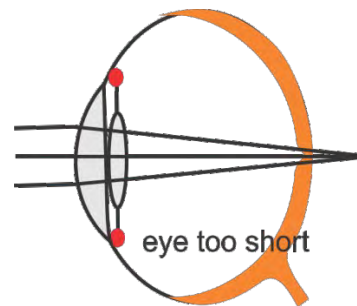
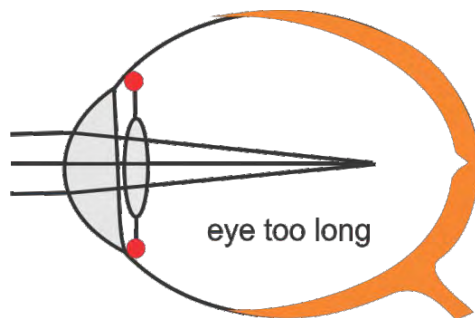
The lens is attached to the ciliary muscles by springs. When the ciliary muscles contract, its diameter decreases, allowing the springs to become less taut and the lens to spring back to its normal round shape thus allowing a close object to be focused onto the retina.



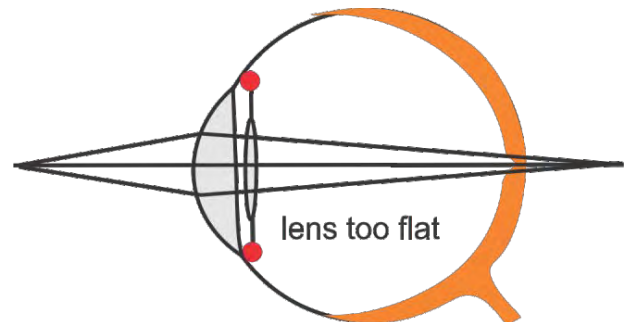
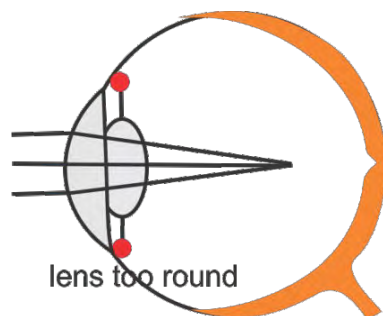
When the ciliary muscles are relaxed, the lens becomes more flat and a distant object is focused onto the retina.

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

i) The shape of the eye ball.



ii) The shape of the lens



Either of the above produces someone who cannot focus on far targets, is **near-sighted**, and needs a **concave** lens.



Either of the above produces someone who cannot focus on near targets, is **far-sighted**, and needs a **convex** lens.



As one gets older, the lens loses its elasticity and remains too flat even when the ciliary muscles are completely contracted. When this happens, images of near objects are blurred.

The Iris

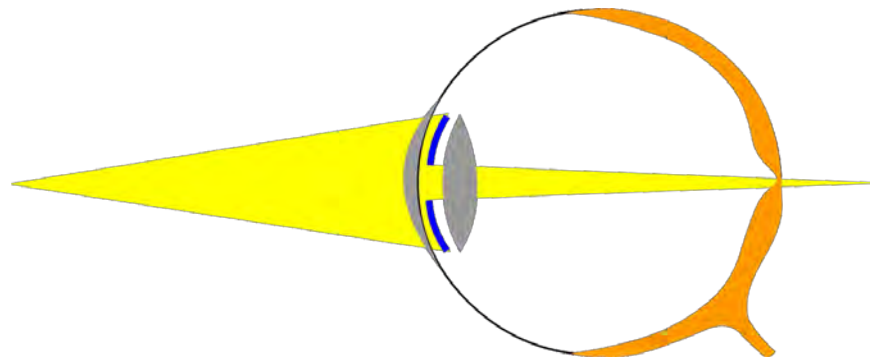
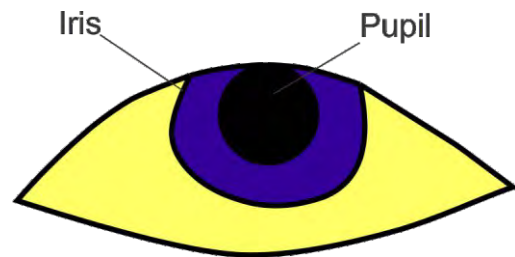
When the lighting is bright, the **iris** constricts and the aperture (the **pupil**) through which light enters the eye becomes smaller.

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 focused 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.



What do the cells in the retina do?

The five cell types in the eye are.

1. The light sensitive receptors are the input layer - **Rods** (R) for black and white and **Cones** (C) for colour.
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 converge signals from peripheral rods.

What is unique about the effect of light on rods and cones?

Light hyperpolarizes these cells (i.e. the voltage inside drops).

Darkness depolarizes them (i.e. the voltage inside rises).

Thus dark acts like a stimulus.

Which cells produce action potentials?

Some amacrine cells and all ganglion cells produce action potentials.

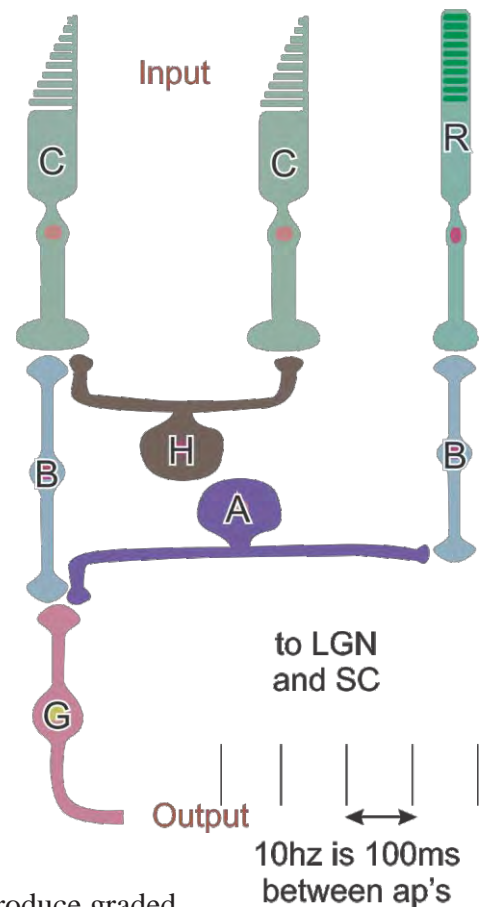
Rods and cones, horizontal cells and bipolar cells only produce graded changes in potential.

Why do most cell types in the eye show only graded changes in potential?

Action potentials (ap's), because they are all or nothing or discrete, are slow at transmitting information. Suppose a ganglion cell fires at 10 hz: an ap every 100ms. Then down-stream structures must wait at least 100ms before they can detect that the frequency has decreased: i.e. that the light level has changed. Graded changes allow continuous and rapid transmission of information.

Why must ganglion cells generate action potentials?

Ganglion cells must transmit information over a long distance to the **Lateral Geniculate Nucleus** (LGN) and **Superior Colliculus**. Graded changes in potential could not travel over such long distances. Ganglion cells must convert visual information, coded by graded potential changes in bipolar cells, into a discrete ap frequency code.¹

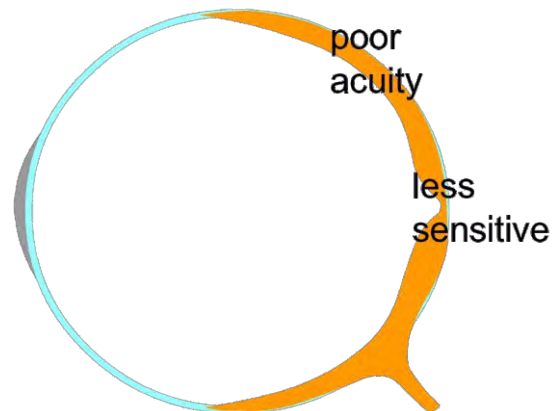


Why is reading difficult in low illumination?

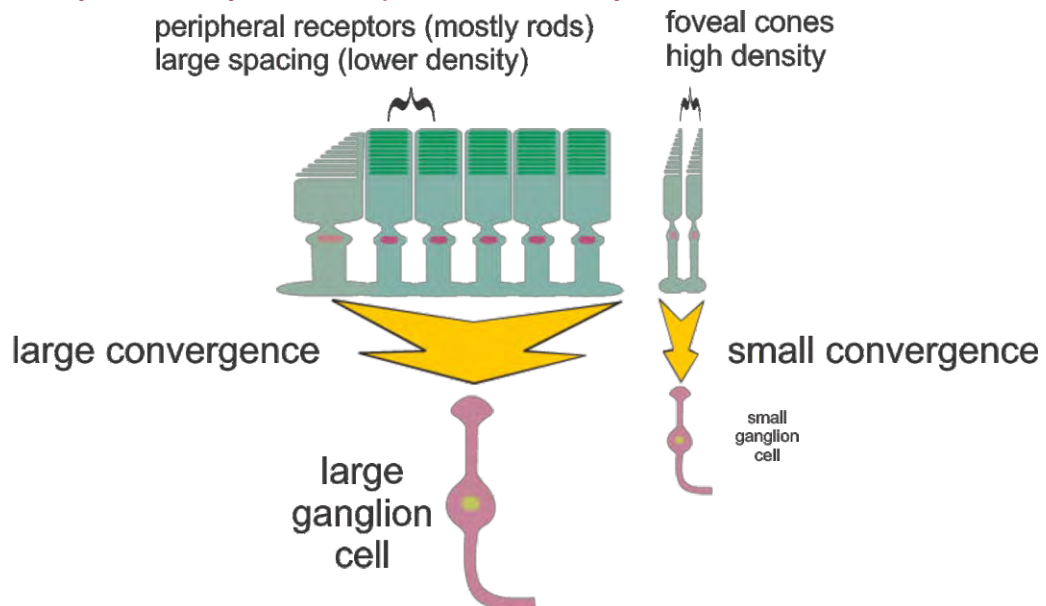
Part 1 of the answer is that the retina is not uniform. The peripheral retina contains primarily rods. The fovea, in the center of the eye, contains only cones

Part 2 is that the rods and cones are not equally sensitive to low light levels. Cones are less sensitive to light. When looking at dim stars, one can see stars in the periphery but they disappear when you look at them with your fovea. In very low levels of illumination, we see only with our rods and therefore see greys not colors.

Part 3 is that the periphery has poor acuity. Try to make out the words of this sentence while staring here *. Why is that?




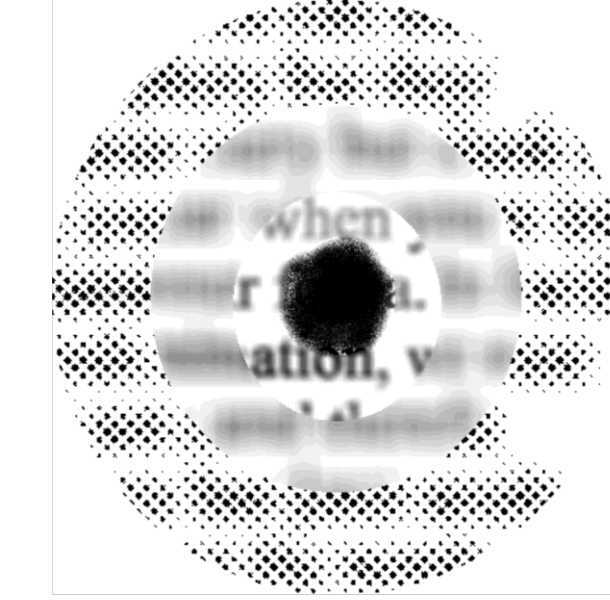
Two reasons why the rod system has poor visual acuity.



1. Large ganglion cells integrate information from a large area of retina
2. Large spacing and large convergence results in low acuity.

1. Small ganglion cells integrate information from a small area of retina
2. Small spacing and low convergence results in high acuity.

What the eye sees

<p>By daylight, only the central fovea sees in detail and in colour.</p>	<p>On a dark night, only the periphery sees, only in black & white, and with poor resolution. The fovea is blind.</p>
	

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.

Define receptive field.

The “**receptive field**” is a very important concept which applies to all senses.

In the eye it explains how information from 100 million rods and cones is funneled down 1 million ganglion cells.

Definition of the receptive field of a ganglion cell:

“That area of retina over which light stimuli changes the activity of a particular ganglion cell.”

The receptive field shows which rods & cones are connected to the ganglion cell.

How would one measure the receptive field of a ganglion cell?

1) Record from a ganglion cell, 2) shine a small beam of light over different parts of the retina in sequence and 3) map those that produce a change in firing rate.

Things to note:

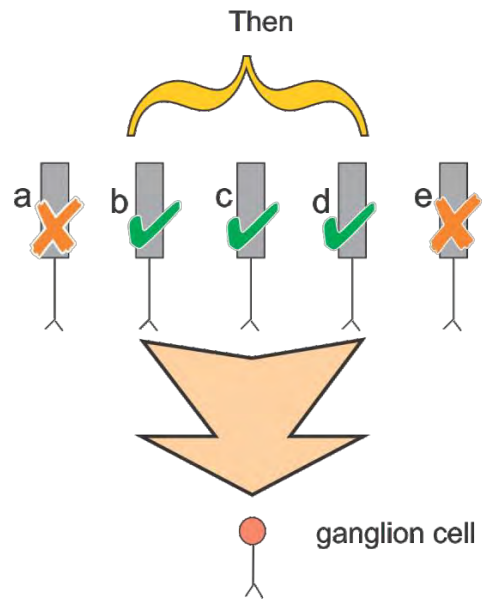
Changes can be excitatory or inhibitory. The same definition applies to other visually responsive cells.

The shape and other characteristics of the receptive field are very important in categorizing cell types.

A similar definition applies to other sensory modalities. E.g. for touch, the skin replaces the retina.

When light is shone on rods b, c, or d, a change is seen in the ganglion cell's firing rate.

When light is shone on a or e no change is seen in the ganglion cell.



b, c, and d are in the receptive field of this ganglion cell

a and e are out of the receptive field of this ganglion cell

Describe the shape of the receptive field of ganglion cells.

What are the two major types of receptive fields of retinal ganglion cells?

1. ON centre, OFF surround
Measure relative brightness
2. OFF centre, ON surround
Measure relative darkness

The figure shows an example of an **on centre cell**.

In b, a light in the centre produces an increase in firing frequency in the ganglion cell.

In c, a light produces a decrease in firing frequency.

An **off centre cell** would have the + and - signs reversed.

What stimulus produces the greatest response?

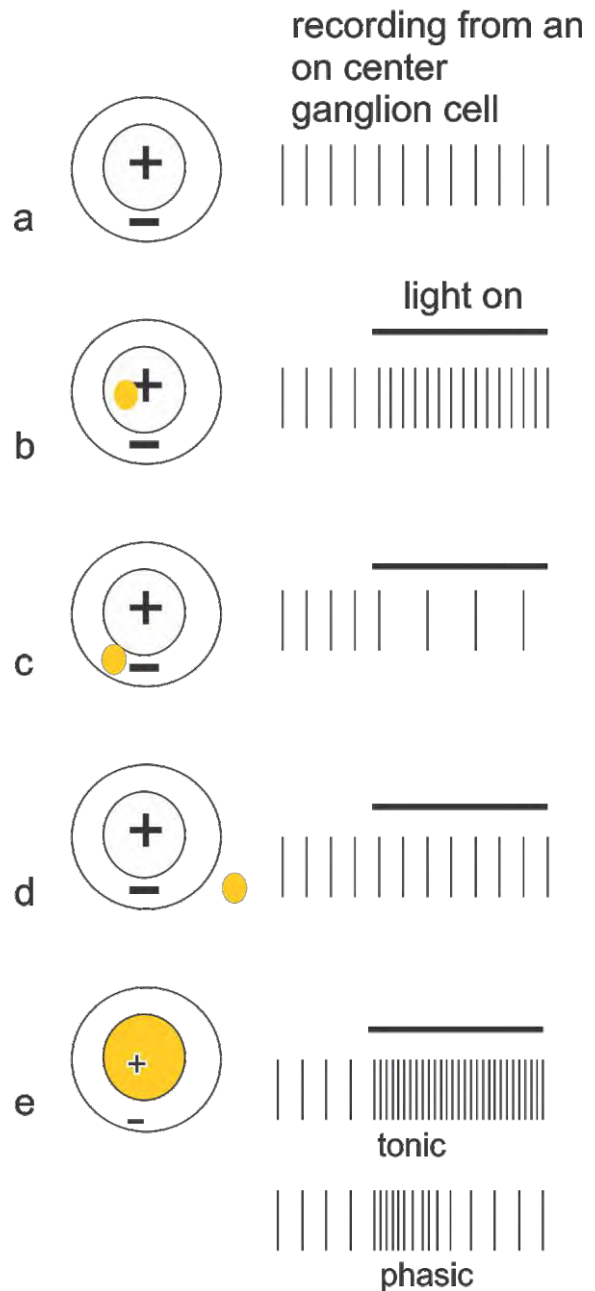
When the light completely fills the on region, as in e.

Draw the response of a rapidly adapting or phasic ganglion cell.

When the light is turned on, the cell fires rapidly for a short period of time. When light is turned off, the cell activity is briefly inhibited.

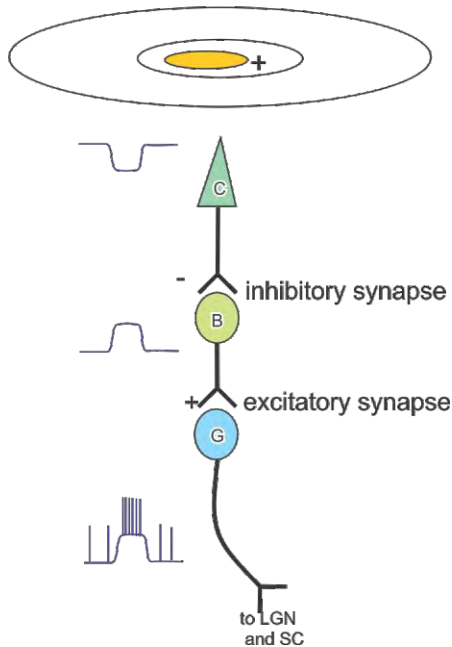
These are good cells for detecting changes such as a flashing light.

● spot of light on retina

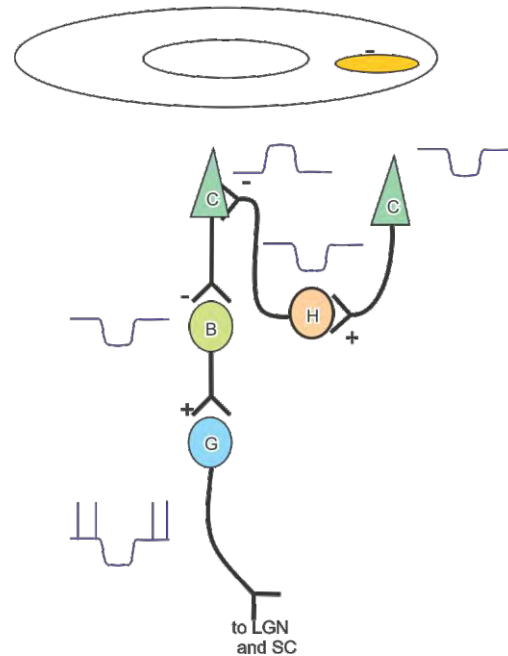


How an antagonistic surround receptive field is produced.

Light to a cone in the centre produces excitation of the ganglion cell.



Light to a cone in the surround produces inhibition of the ganglion cell.



This is because:

- 1) light decreases the cone voltage and the cone releases less inhibitory transmitter.
- 2) the voltage inside the bipolar cell increases and it releases more transmitter.
- 3) the ganglion cell is excited and it fires more often.

This is because:

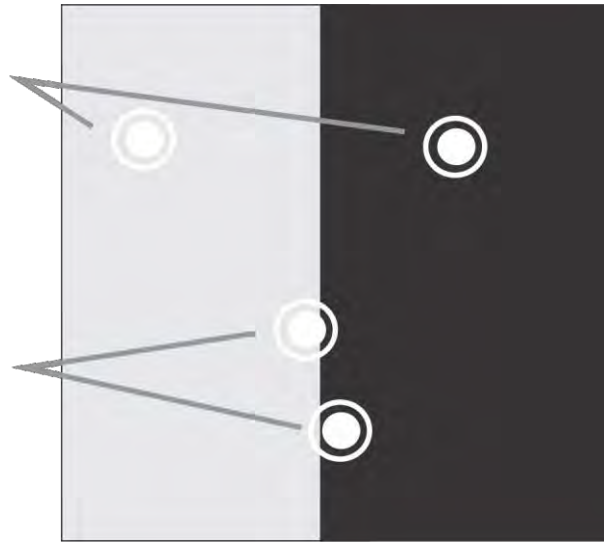
- 1) light decreases the surround cone's voltage and the cone releases less excitatory transmitter.
- 2) the voltage inside the horizontal cell decreases and it releases less inhibitory transmitter.
- 3) the voltage inside the centre cone increases and it releases more inhibitory transmitter.
- 4) the voltage inside the bipolar cell decreases and it releases less excitatory transmitter.
- 5) the ganglion cell is inhibited and it fires less often.

The Function of Antagonist Surround in Ganglion Cells

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 increased or decreased



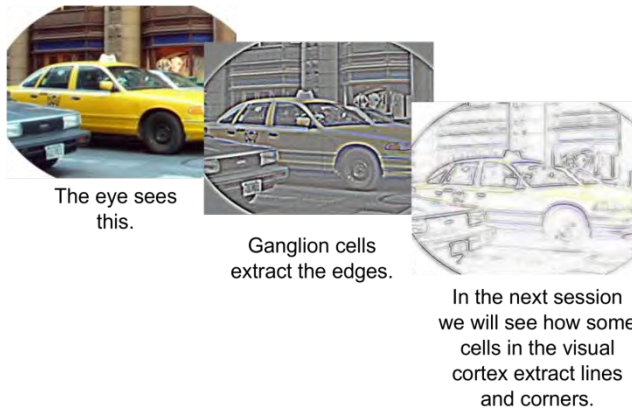
Recall Question 1: How does the brain compute what it must using so few active neurons?

By activating only ganglion cells that sense a change, i.e. the edges, the brain keeps the number of active neurons to a minimum.

This is similar to computer compression software used to transmit large images along the Internet. Suppose you were transmitting the color of a series of dots along the internet, each colour coded by a number from one to 2000000. The series uncompressed would look like:

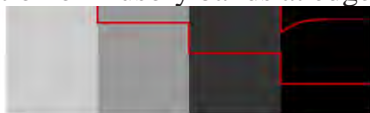
1756333, 1756333, 1756333, 1756335, 1756335, 1756333 Compressed, by coding only changes in color, it would look like: 0,0,2,0,-2..... a lot shorter.

Vision involves extracting key features.

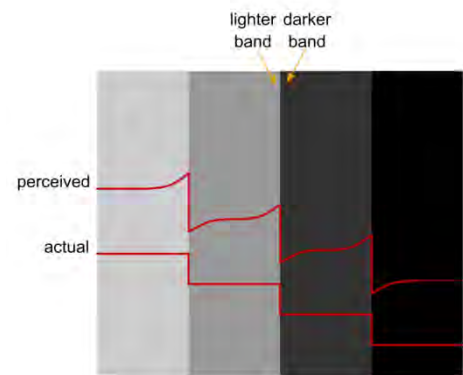


The consequence of edge extraction

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



Often artists create this phenomenon to further enhance an edge as in the "Woman Seated at an Easel" by Georges Seurat.



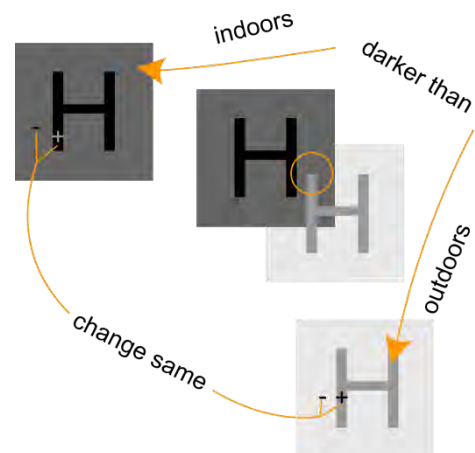
By measuring change, ganglion cells also provide constancy.

The black letters on a page should look black indoors or outside in the sun.

Yet the white paper indoors reflects less light (is more black) than the black letters outdoors.

Because of constancy, the white page does not turn black.

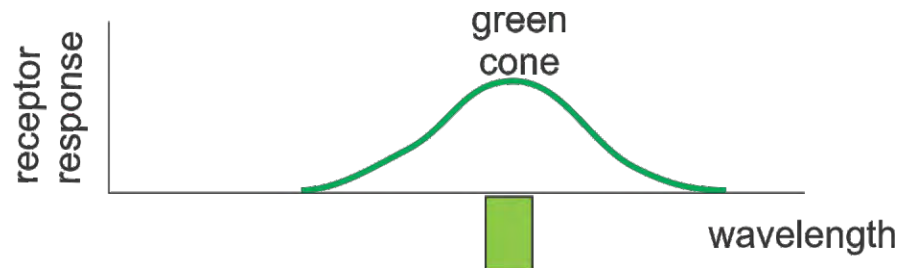
The absolute amount of ambient light is largely irrelevant. By measuring change, ganglion cells remove this redundant information. The contrast, or change in intensity between adjacent bits of an image, remains constant independent of lighting conditions.



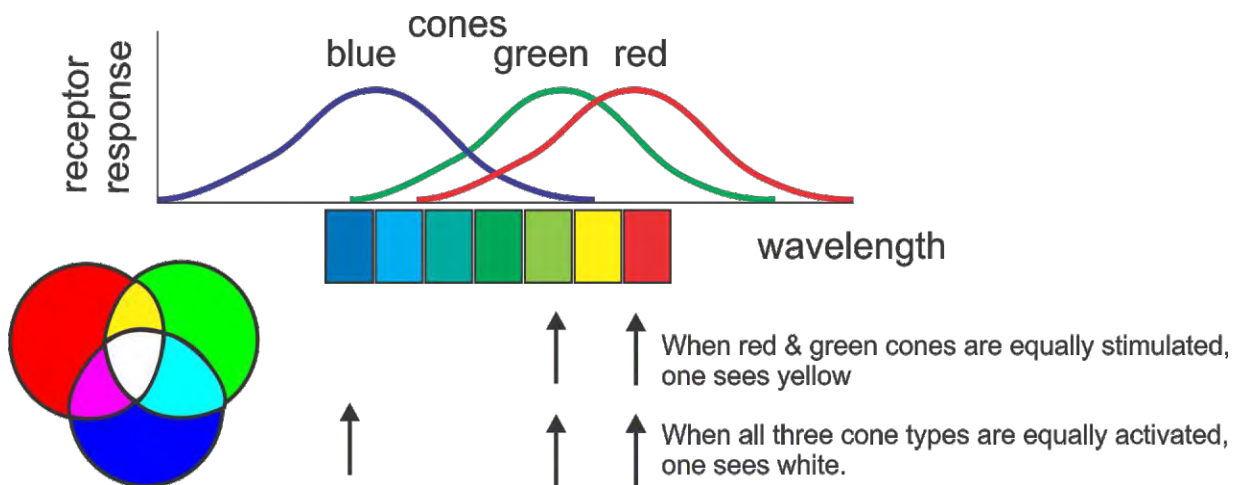
What is the advantage of colour vision?

The sense of color developed in order to see which fruit is ripe. Cones respond better to a particular wavelength of light than to others.

The one shown below responds best to green light.



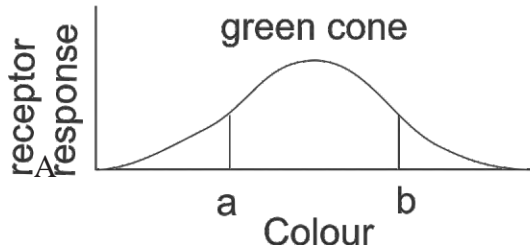
We have three cone types.



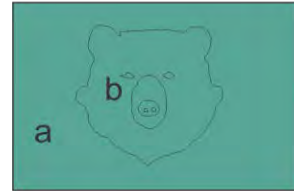
Show how a two colour cone system is better at distinguishing an object from its background.

An object “b” (perhaps a brown bear) is not visible against the background “a” because both produce the same receptor response. Not very good survival value.

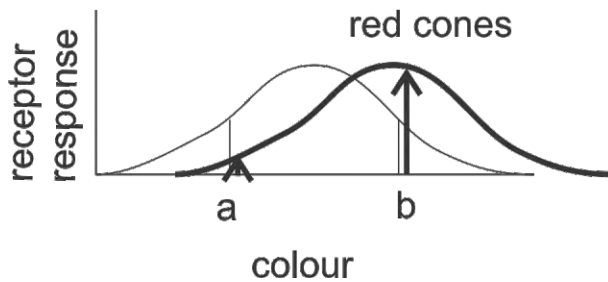
Spectral sensitivity of one cone.



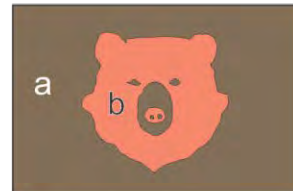
green cones see



Adding a red cone is good because red cones respond differently to the colours “a” and “b” and one can see object b against the background a.



red cones see



Most species have evolved at least a two cone system. In some cases, a two cone system can still be fooled. To overcome this, some species, like humans, have evolved a three cone system.

How cones are distributed on the retina

In the fovea,

1) the # of each cone type is not equal. Usually red cones are most numerous and blue cones least numerous.

2) the relative #'s vary from person to person.

3) the cones of the same type form clusters.

The very centre of the fovea has no blue type cones.

As one moves away from the fovea,

1) the #'s of cones drops and the #'s of rods increases.

2) the size of both rods and cones increases and thus their density (# per square mm) decreases.

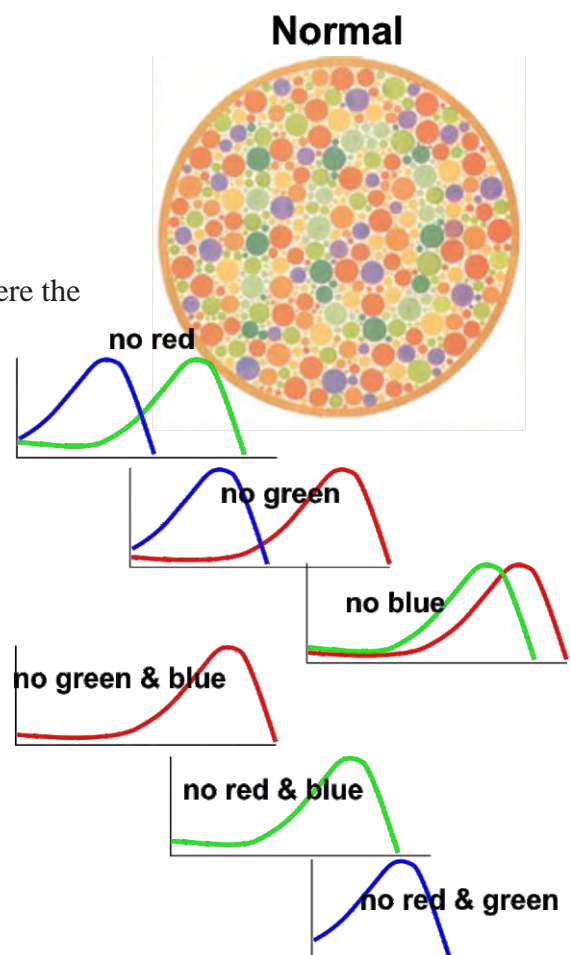
3) cones become larger than rods.

Colour blindness

Do you see a "10" composed of green dots? Here the green color is the main distinguishing features between the dots that form the "10" and the background. If you do not see the "10", you may be color blind. But another possibility is that colors used to reproduce this figure are not quite correct.

Each cone type contains a different light sensitive photo pigment. Colour blindness occurs when there is a defect in the genes that produce these photo pigments. Various combinations of defects can occur.

- 1) Missing one cone type
- 2) Missing two cone types
- 3) Missing all three cone types (vision is limited to the rods)
- 4) A cone type is made with a photo pigment different from normal.



How many gradations of color can the human brain distinguish?

a) 200 hues

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

hues



b) 20 levels of **saturation**

Combinations of two more wavelengths. When complementary wavelengths are combined equally, one gets grey.



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 we can see $500 \times 200 \times 20 = 2,000,000$ gradations of colour.

Not bad with just 3 cone types!

An experiment on colour adaptation

Stare at the "x" for 10 sec then look at the blank right side. You should see a faint after-image of the same circles but in different colors. To recharge the after-image look at the "x" again.

You should see after-images.

The red circle leaves a pale green after-image. Green leaves pale red.

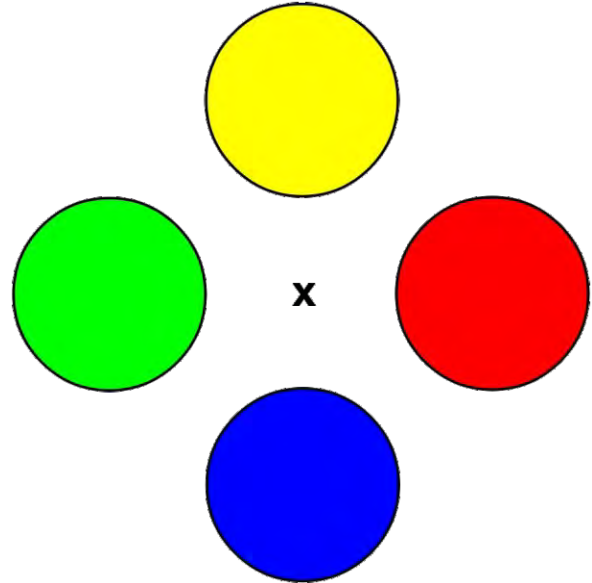
Also yellow leaves pale blue and blue leaves pale yellow. Why?

It suggests that red and green are opposites; that they act as push-pull pairs. Normally white light activates both equally.

During prolonged viewing of the red spot, the signal from the red cones adapt. If you now look at white, the push from red is weaker than the pull from green. The result is that you see a pale green.

Similarly yellow and blue are push-pull pairs.

The story of how push pull pairs are formed begins with the ganglion cell, on the next page.



Cells that receive input from cones

Two main types are.

1) *Non-opponent cells*

The first is the center surround ganglion cell that we saw earlier in this session. These are on- or off- center and receive input from one or more of the cone types.

This type comes in a variety of flavors. Shown here are three. What property do they all share?

1) The center and surround contain the same combination of cone types. For this reason they are called non-opponent cells.

2) The influence of the center is the opposite of the surround.

This makes these cells good at detecting a change in the brightness between the center and surround.

Surprisingly like cones, they are not very sensitive to a change in color.

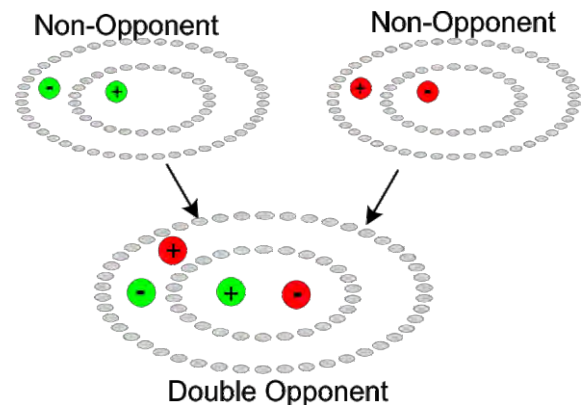
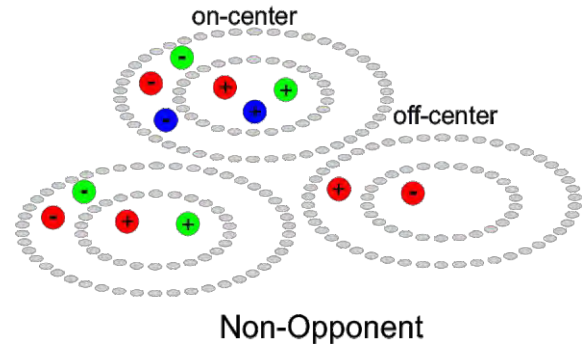
2) *Double opponent cell*

This cell type is not found in the eye but in the part of the cerebral cortex that receives information from the eye.

Its receptive field is formed by combining information from non-opponent ganglion cells.

One also finds blue - yellow double opponent cells.

It is somewhat surprising that by combining two receptive fields that are not color sensitive one obtains a receptive field that is very color sensitive.



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 single opponent cell will respond not only to pure red but also to yellow. This double opponent cell will only to red.

Adaptation of double opponent cells

Recall how prolonged viewing of a red spot made white look green. Prolonged exposure to red light in the center will adapt the red more than the green cones. Now when exposed to white light, the influence of the green cones will exceed that of the red cones and activate the double opponent cell. The result is the perception of green.

Thus because we have red green double opponent cells the after-image of red is green and vice versa. Similarly because we have yellow blue double opponent cells the after-image of yellow is blue and vice versa.

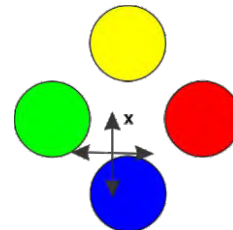
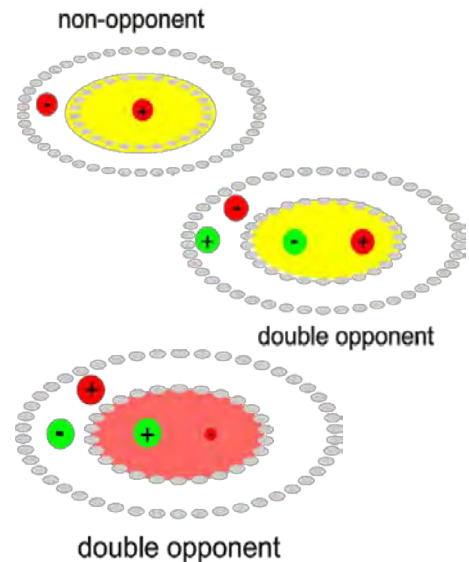
Non-opponent cells are good at distinguishing differences in brightness.

Double opponent cells are good at distinguishing differences in hue and saturation.

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

A green spot in the centre activates the double opponent cell. A red spot in the surround also activates the cell.

A combination of the two gives the maximum response. This is why a green tie against a red background really stands out. Other double opponent cells would be maximally activated by a yellow tie against a blue background.



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.

How does this help maintain colour constancy?

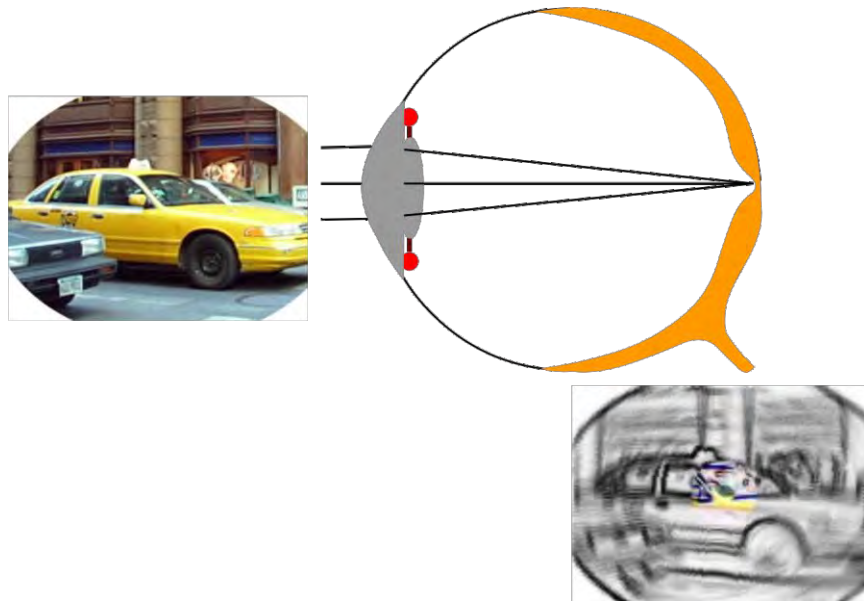
Because the centre and surround produce opposite responses, such a cell is unaffected by any background colour (e.g. diffuse yellow light over the centre and the surround) and thus maintains colour constancy.

What happens when you expose outdoor film indoors?

Your pictures will have a yellow hue from the background incandescent lights. Film measures absolute colour and does not have colour constancy.



In Summary



The eye does three things.

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

Compression occurs in two ways.

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

Thus the many receptors of the retina activate only a few neurons in the cortex. The title of this Course is “Transformations for Action and Perception”

In this lecture we have learnt that the neurons of the eye transform the visual image in a number of ways. Surprisingly the result seems like a very poor replication of what is there. Yet we perceive the world with amazing clarity, or at least we think we do. How the cortex achieves this perception is the subject of the rest of the course.

See problems and answers posted on

<http://www.tutis.ca/Senses/L1Eye/L1eyeProb.swf>