The Physiology of the Senses
Lecture 1 - The Eye

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Contents

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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 cone receptors in the retina are not adequate for distinguishing colors.

Introduction

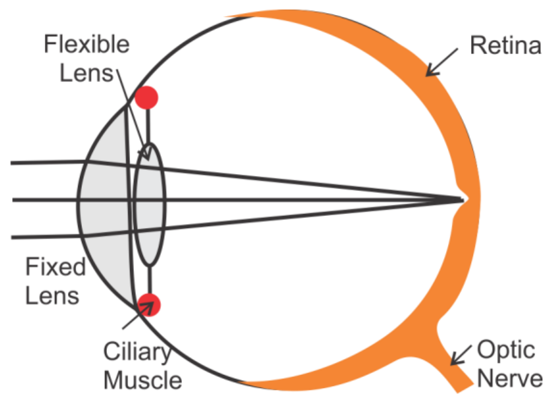


Figure 1.1 Light is focused 1st by the fixed lens and 2nd by the flexible lens onto the retina at the back of the eye. Neurons in the retina project down the optic nerve to the brain.

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

Most people believe the myth that humans use only 10% of their neurons. One’s goal in life is to increase this number. The truth is that the brain uses 100% of its neurons.

However, the cost of a single action potential is high. If you activate much more than 1 or 2 % of your neurons at the same time, about 1 to 3 billion neurons, you would faint from a depletion of the brain’s oxygen (Lennie 2003). Our brains have evolved to be very efficient. An iMac consumes 150 watts of energy (3 standard light bulbs). The human brain consumes a mere 20 watts (40 % of one standard light bulb). 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. In this lesson we will start with the eye. The eye is a good place to start because the eye’s neurons are an outgrowth of the cortex.

Let’s begin with the three 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 that convert light to electrical activity.

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

The eye is the brain’s window on the world. As well, because the retina is part of the cerebral cortex, it is the doctor’s window into the brain. New techniques are now being developed to use our view of the retina to spot early signs of dementia such as Alzheimer’s disease (Hart et al 2016).

Accommodation

Light is focused by the curvature of two lenses: a fixed lens (cornea) and a flexible lens.

The curvature of the flexible lens is changed by the donut shaped **ciliary muscle** that encircles the lens.

The lens is attached to the ciliary muscle by springs. When the ciliary muscle contracts, 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 (Figure 1.2A).

When the ciliary muscle is relaxed, the lens becomes more flat and a distant object is focused onto the retina (Figure 1.2B).

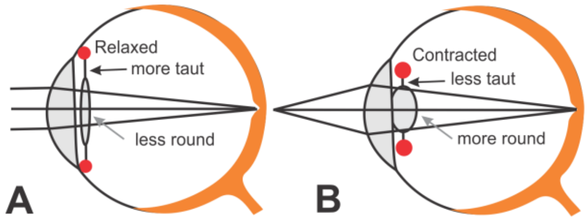
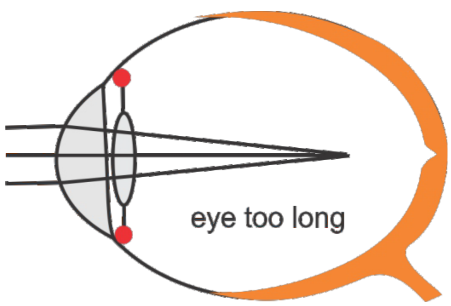
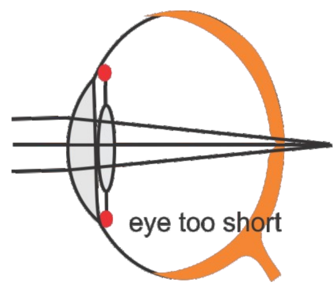


Figure 1.2 The ciliary muscle changes the curvature of the flexible lens. A. To view a far target the muscle relaxes and the springs pull on the lens making it less round. To view a near target the muscle contracts releasing the lens allowing it to return to its normal round shape.

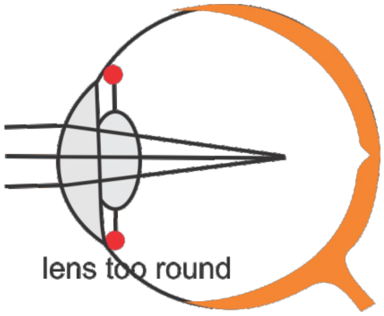
One's ability to clearly focus an image depends on two factors.

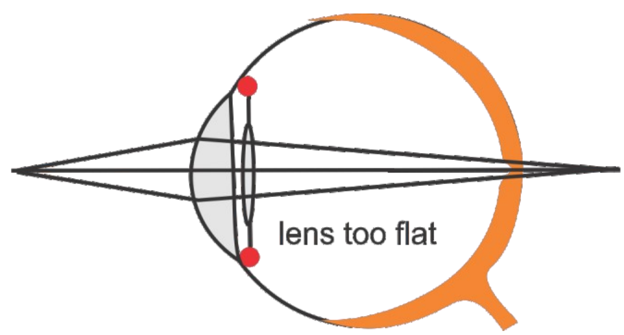
1) *The shape of the eye ball*
(Wallman & Winawer 2004)





2) *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)** becomes smaller and less light enters the eye. 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 (Figure 1.4). Normally when the pupil becomes smaller in diameter, the area of blur on the retina becomes smaller. Infact, 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.

Figure 1.3 The iris (brown) determines the diameter of the pupil (black).

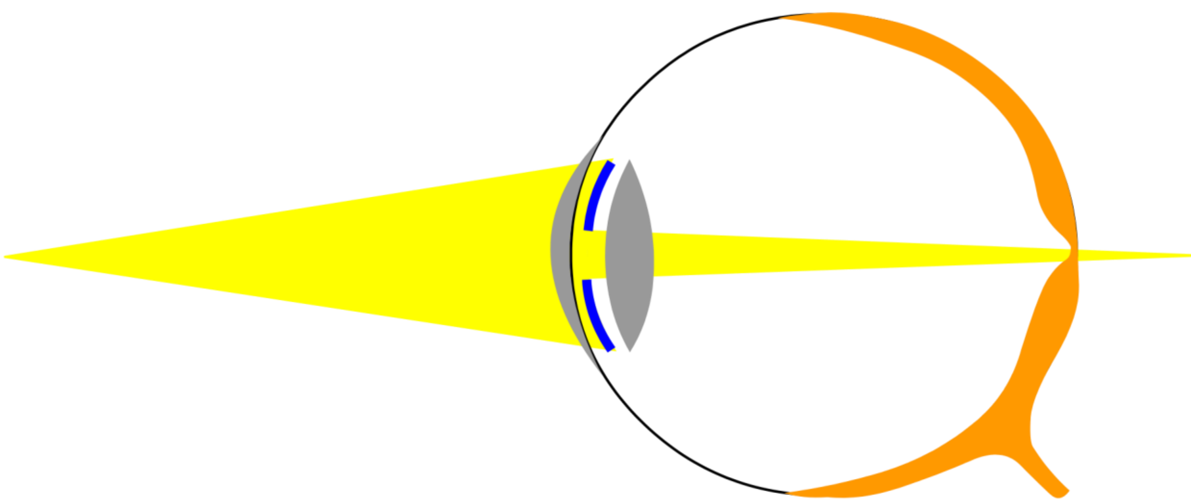


Figure 1.4 A pupil of a small diameter reduces the blur on the retina.

The Cells in the Retina

The retina on the back of the eye contains a network of cells which change light into voltage and funnels this electrical activity down the optic nerve to the cortex. The five cell types in the retina are:

1) The light sensitive receptors are the input layer - **Rods** (R) for black and white and **Cones** (C) for color.
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 via bipolar cells.

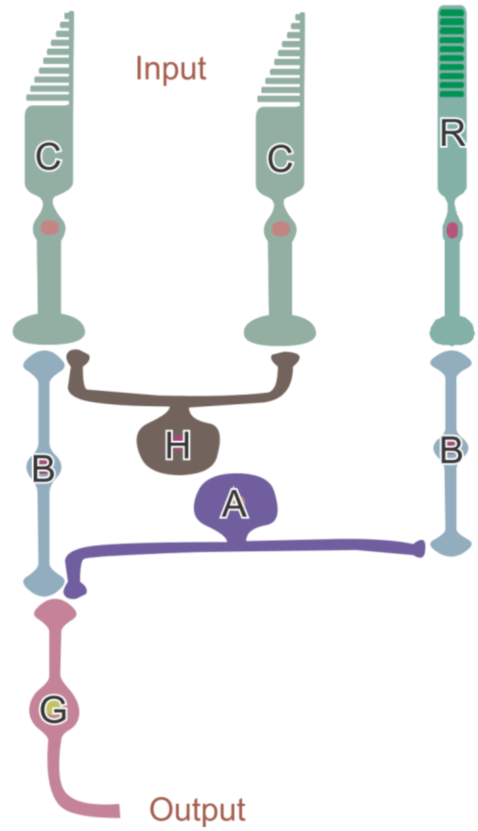


Figure 1.5 The Cell Types in the Retina Light activates the receptors consisting of rods (R) and cones (C). These connect through bipolar (B) cells onto ganglion (G) cells. Horizontal (H) cells and amacrine (A) cells interconnect receptors and bipolar cells.

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?

Ganglion cells produce short-lasting changes in voltage called action potentials that travel down the axon to the cortex. Action potentials (ap's), because they have a relatively small frequency of about 10 to 1000 per second are slow at transmitting information. Why is that? Suppose a ganglion cell fires at 10 hz: an ap every 100ms. Then down-stream structures must wait until the next action potential, about 100ms, before they can determine if the frequency has decreased or increased: 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 code consisting of action potentials.

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?

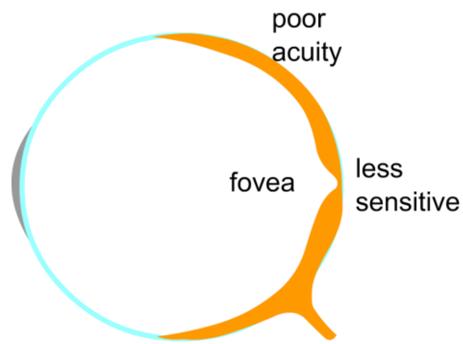


Figure 1.6 The retina (orange) is less sensitive to light in the fovea and has poor acuity in the periphery.

Two reasons why the rod system has poor visual acuity

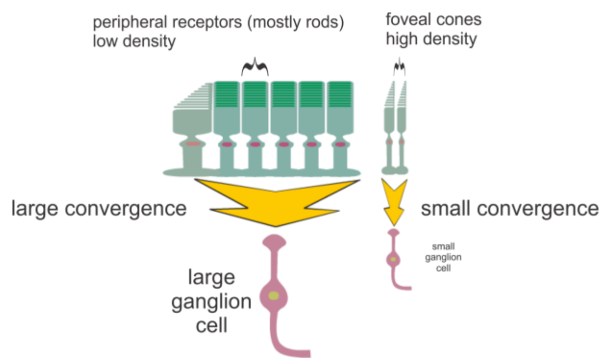
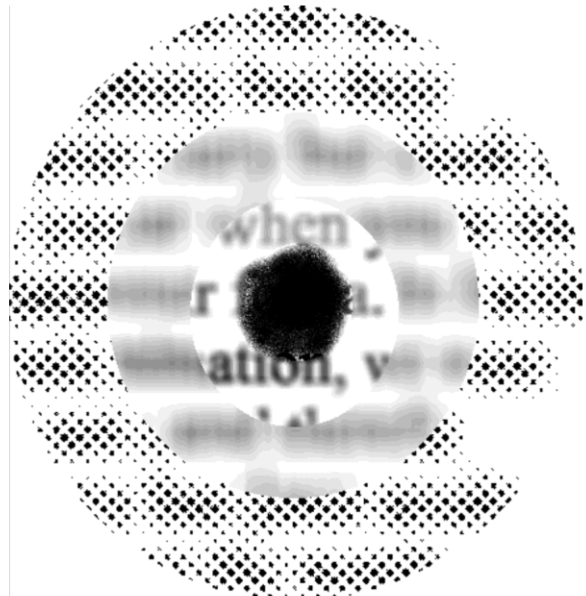


Figure 1.7 A Comparison of the Peripheral and Foveal Retina Large ganglion cells in the peripheral retina have poor acuity because of a large convergence of low-density receptors. Small ganglion cells in the fovea have a high acuity because of a small convergence of dense cones.

Left	*Right*
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 in detail and in color.	On a dark night, only the periphery sees, only in black and white, and with poor resolution. The fovea is blind. The proper function of the rods is essential for **night vision**.
 **Figure 1.8 What the Eye Sees by Daylight**	 **Figure 1.8 What the Eye Sees by Moonlight**

The optic nerve is small compared to the large retina and thus 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 2 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.

Receptive Fields

The "**receptive field**" is a very important concept which applies to all senses. It is the neuron's window to the world.

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

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 and 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 all visually responsive cells.

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

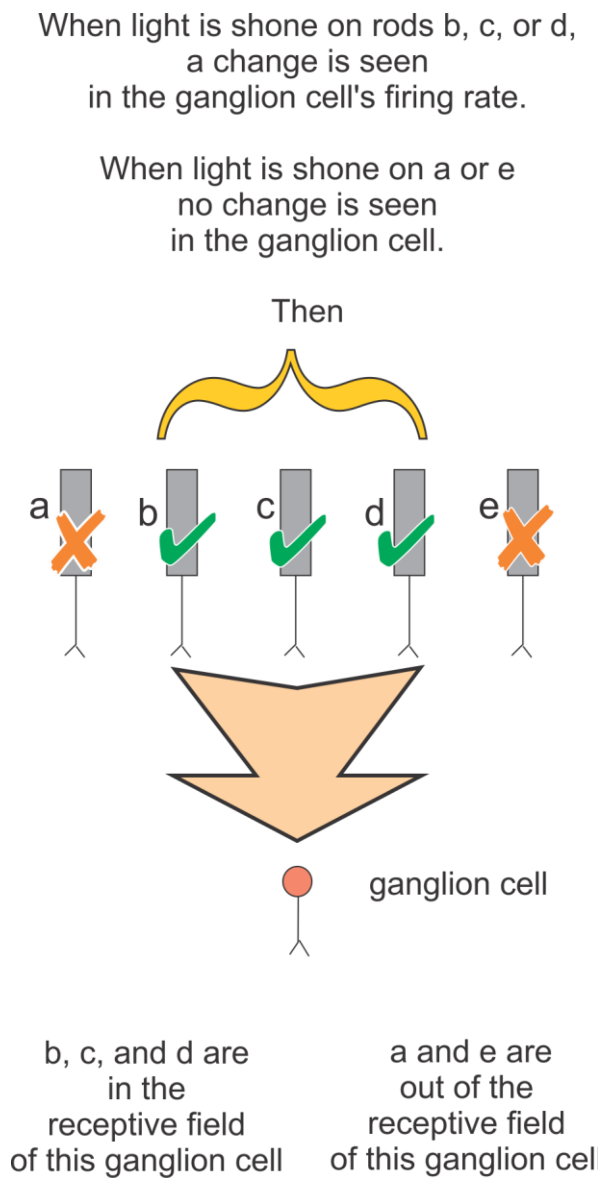


Figure 1.9 The receptive field of the ganglion cell consists of receptors b, c, and d.

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

Describe the shape of the receptive field of ganglion cells.

The receptive fields of retinal ganglion cells come in two flavours.

1) ON centre, OFF surround
Measure relative brightness

2) OFF centre, ON surround
Measure relative darkness

Figure 1.11a 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 in the surround produces a decrease in firing frequency.

An **off centre** cell would have the + and - - signs reversed. There are equal numbers of on and off centre cells.

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.

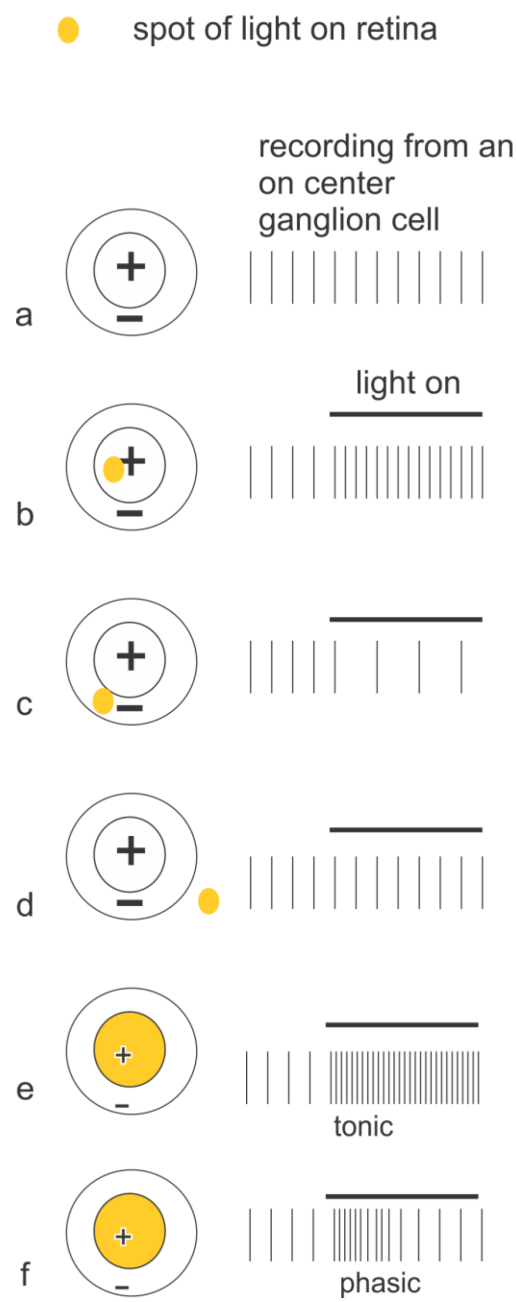


Figure 1.10 Firing rate of an on centre ganglion cell to a spot of light (shown as yellow) on retina a) basal firing rate. b) increased rate to a light in the on centre. c) decreased rate to a light in the off surround d) basal rate to a light outside the receptive field. e) maximum increase to a light that fills the on centre. f) a phasic response to a light stimulus.

How an Antagonistic Surround Receptive Field Is Produced

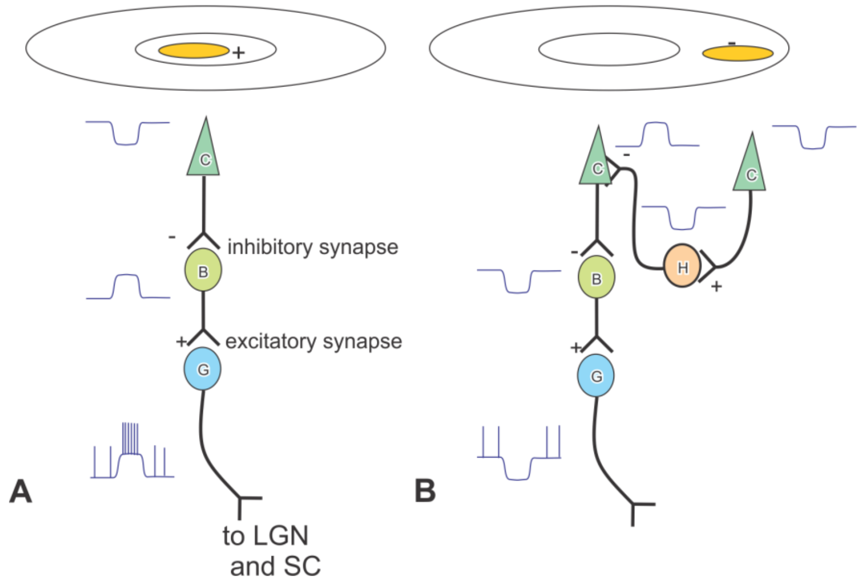


Figure 1.11 **Synaptic Connections of an On Centre Ganglion cell** A) Light to the centre produces excitation of the ganglion cell. B) Light to the surround produces inhibition of the ganglion cell.

A) In the on centre:	B) In the off surround:
1) light decreases the cone voltage and the cone releases **less** inhibitory transmitter. 2) less inhibition causes the voltage inside the bipolar cell to increase and it releases more transmitter. 3) the ganglion cell is excited and it fires **more** often.	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 fires **less** often.

The Function of Ganglion Cell Receptive Fields

When the eye sees a black/white edge, the activity of ganglion cells far from the edge shows a similar low level of activity. This is because both centres and surrounds cancel.

Only at the edge is the activity increased or decreased.

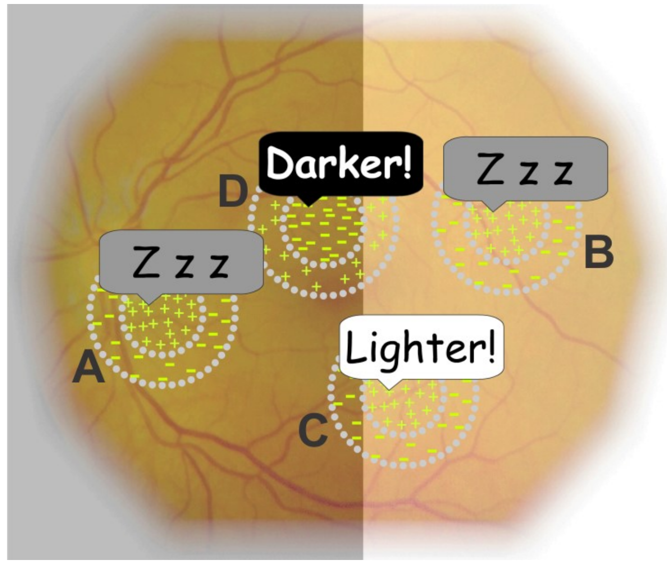


Figure 1.12 A change in response is seen only when the receptive field is near the black/white edge. The eye's ganglion cells A and B fire at their basal rates because the centre and surround responses cancel. Less inhibition from the edge in the dark occurs in C. More excitation from the edge in the light occurs in D producing an increase in firing rate and thus highlighting the edge.

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

The answer is: by activating only ganglion cells that sense a change, i.e. the edges, the brain keeps the number of active neurons to a minimum.

In summary: vision involves extracting key features.

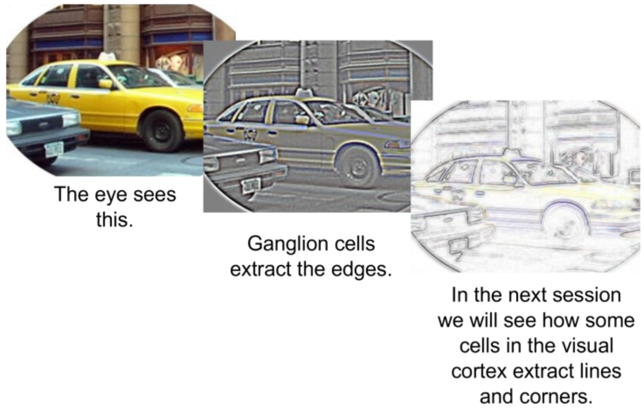


Figure 1.13 The Features Extracted at Various Stages From left the right: What the retina "sees". What the ganglion cells respond to. What the visual cortex extracts.

The consequence of edge extraction

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

Note the darker and lighter bands in the grey black border (Figure 1.15B). These bands are not really there. Often artists create this phenomenon to further enhance an edge as in the "Woman Seated at an Easel" by Georges Seurat (Figure 1.15A). The brain does the same in order to accentuate the shape and identity of objects.

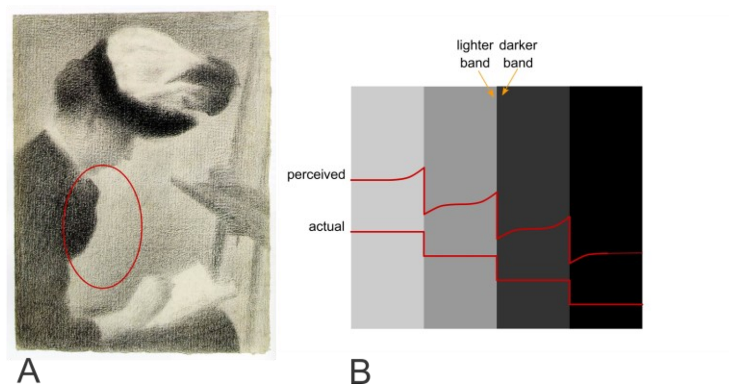


Figure 1.14 Accentuating Edges A) George Seurat darkened the dark edge and lightened the light edge inside the red ellipse. B) inhibitory surround produces an illusion of an accentuated edge.

By measuring change, ganglion cells also provide constancy.

The black letters on a page should look black indoors or outside in the sun. The same should hold for a white page.

Yet the white paper when viewed 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.

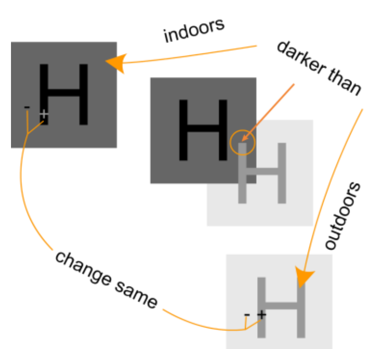
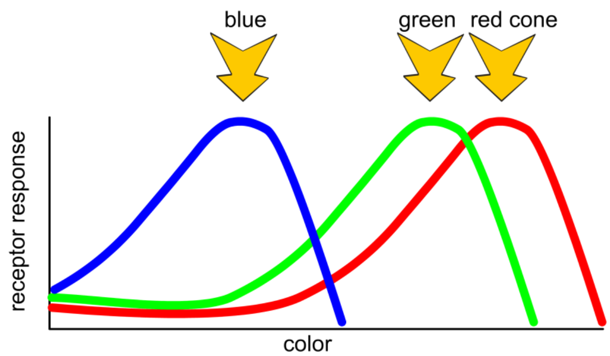


Figure 1. 15 Black-and-White Constancy The black of a letter seen outdoors is lighter than the white of the paper seen indoors.

Advantages of Color Vision

The sensation of color developed, in part, to allow us to see which fruit is ripe (Wolf 2002). Cones (Figure 1.17A) respond best to a particular wavelength of light and respond, but less, for a large range of colors. We have three cone types, blue, green, and red color sensitive.

A



B

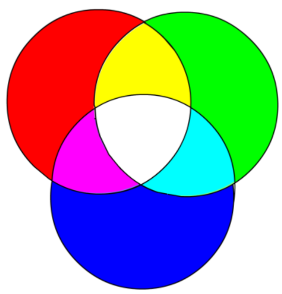


Figure 1.16 A) The Response of the Three Cones Types to Different Colors (wavelengths of light). B) Mixing light is not the same as mixing paint. Combining these shades of red and green lights yields a yellow light. Mixing these shades of red, green and blue lights yields a white or grey colored light.

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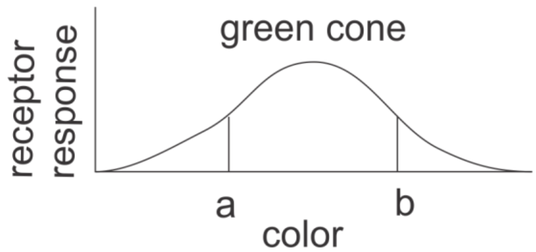
A three color cone system is good at distinguishing an object from its background.

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



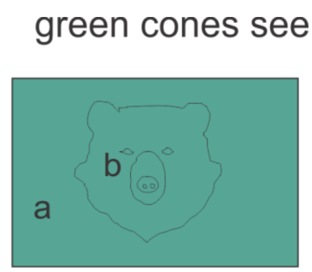
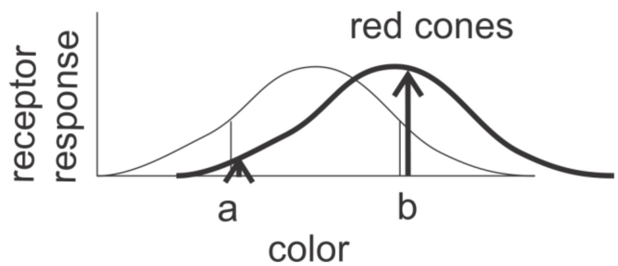


Figure 1.17 Left: the response of a green cone to colors a and b are the same. Right: an object of color b is not visible against a background of color a.

Adding a red cone is good because red cones respond differently to the colors “a” and “b” and object b stands out against the background a.



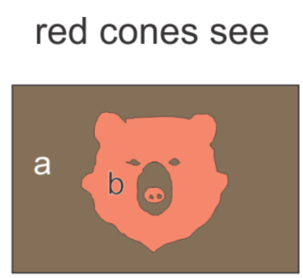


Figure 1.18 Left: the response of a red cone to colors a and b are different. Right: an object of color b is now visible against a background of color a.

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. However even our three cones are not very good at distinguishing between colors. This is because each cone is responsive to light over a wide range of colors.

If the activity of a cone changes, is this due to a change in color or brightness? We will see soon how this problem is resolve by special color sensing cells in the visual cortex.

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 # of cones drops and the # of rods increases.

2) the size of both rods and cones increases and thus their density (# per square mm) decreases(Roorda & Williams 1999).

Color 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.

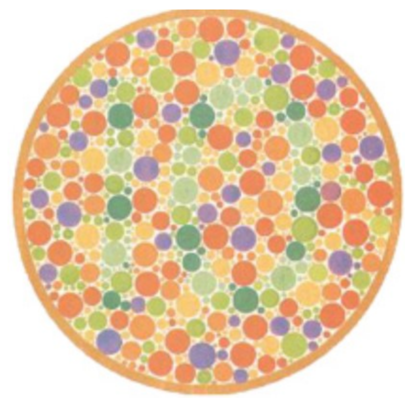


Figure 1.19 A Test for Color Blindness. If you can see the 10 that is in green, your green cones are working.

Each cone type contains a different light sensitive photo pigment. Color 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
- The patient has only peripheral, not foveal, vision.

4) A cone type is made with a photo pigment different from normal.

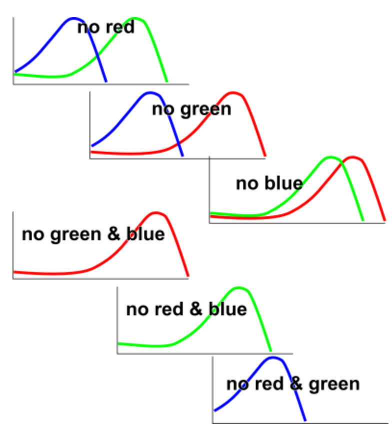


Figure 1.20 Various Types of Color Blindness

How many gradations of color can the human brain distinguish?

Figure 1.21. The hues consist of all the wavelengths of visible light.

a) 200 hues

The brain transforms the wavelengths of light seen in a rainbow into a color circle containing 200 distinguishable hues.

b) 20 levels of **saturation**

Saturation is the combination of two or more wavelengths. Hues on opposite sides of the color circle (those that go through the center) are complementary. When complementary wavelengths are combined equally, one gets grey. Combining green with its non-complementary shade of red produces yellow Figure 1.23).

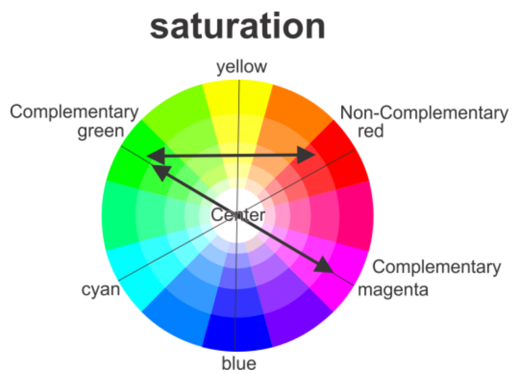


Figure 1.22 When hues of light are mixed different levels of saturation are produced.

c) 500 **brightness** levels

Any color 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.

Figure 1.23 Each level of saturation can be made brighter or darker.

Remarkably we can see 500x200x20 = 2,000,000 gradations of color.

Not bad with just 3 cone types!

An Experiment on Color Adaptation

Stare at the "x" in Figure 1.25 for 10 sec, and 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.

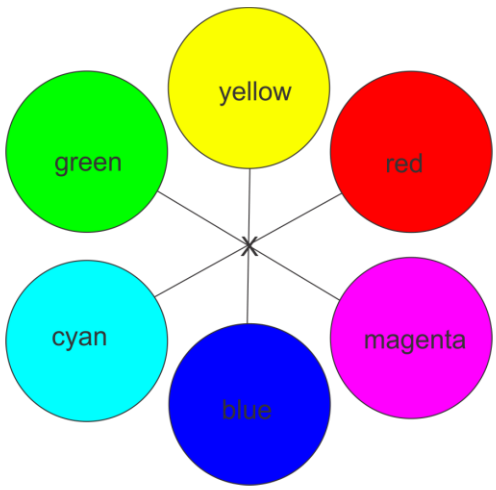


Figure 1.24 **If one stares at the blank area the right after staring at the X for 10 seconds, one observes the complementary colors as an after image.**

The red circle leaves a cyan (light blue) after-image. Green leaves magenta (purple). Also yellow leaves dark blue. Why?

It suggests that complementary colors are opposites; that they act as push-pull pairs. Normally white light activates all cones equally. During prolonged viewing of the dark blue spot, blue cones adapt. If you now look at white, the push from the adapted blue cones is weaker than the pull from yellow (red and green) cones. The result is that white is seen as a dark blue. The story of how push-pull pairs are formed begins with an important cortical cell, on the next page.

Double Opponent Cells

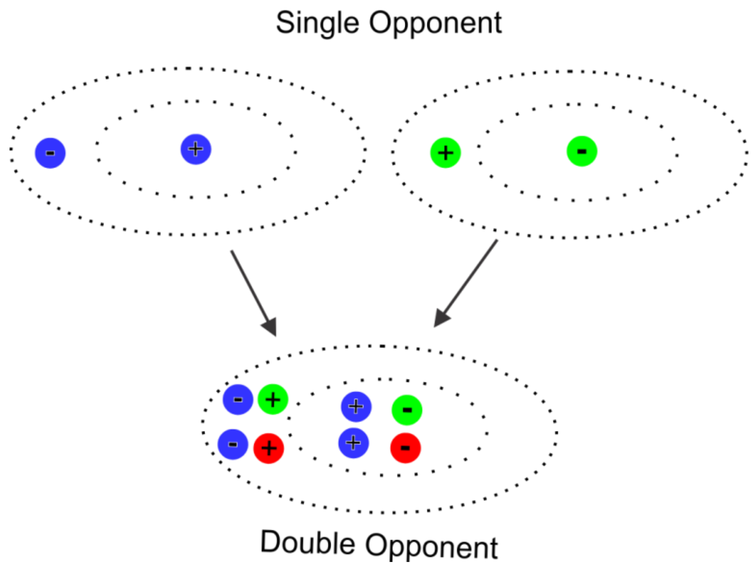


Figure 1.25 The Receptive Field of a Blue-Yellow Double Opponent Cells in the Visual Cortex

The cell type needed is the **double opponent cell**, which is not found in the eye's retina but in the cerebral cortex. Recall that in the retina one finds on-centre and off-centre ganglion cell. One also finds ones driven by one of the three types of cones (Figure 1.26). The receptive fields of these **single opponent** cells (centre vs surround) are combined in the cortex to form **double opponent** cells (centre vs surround and centre vs centre)(Conway 2009, Shapley & Hawken 2011). The centre has an excitation from blue cones that is equal to the inhibition from red and green cones. Thus, white light will not activate this cell. Blue light will activate the centre and inhibit the surround. Yellow light will do the opposite. One also finds green-magenta double opponent cells.

The Advantages of the Double Opponent Cell

Adaptation of double opponent cells

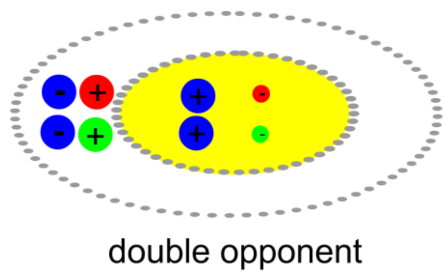


Figure 1.26 Prolonged exposure to a yellow spot produces a blue after-image.

Recall how prolonged viewing of a yellow spot made its afterimage look blue. Prolonged exposure to yellow light in the centre will adapt the red and green cones more than the blue cones (Figure 1.27). Now when exposed to white light, the influence of the blue cones will exceed that of the red and green cones and activate the double opponent cell. The result is the perception of blue.

Thus because we have blue-yellow double opponent cells, the after-image of yellow is blue and vice versa. Similarly, because we have green-magenta double opponent cells, the after-image of magenta is green and vice versa. In fact, if you pick any color around the color wheel (Figure 1.23) you can predict that its after-image color is that on the opposite side of the color wheel, going through the centre.

Why does a blue object against a yellow background stand out so well?

A blue spot in the centre activates the double opponent cell in Figure 1.26. A yellow spot (red and green light) in the surround also activates the cell.

A combination of the two gives the maximum response. This is why a blue tie against a yellow background really stands out. This double opponent cell responds best to the **change** from blue to yellow. Other

Figure 1.27 A yellow tie stands out against a blue shirt.

double opponent cells would be maximally activated by a yellow tie against a blue background (Figure 1.28).

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

Diffuse yellow light over the centre activates both red and green receptors. Yellow light in the surround activates the same receptors cancelling the input from the centre (Figure 1.26). Diffuse blue light does the same, as does any diffuse color.

How does this help maintain color constancy?

Because the centre and surround produce opposite responses (Figure 1.26), a double opponent cell is unaffected by any background color (e.g. diffuse yellow light over the centre and the surround). This property maintains color constancy.

What happens when you do not adjust the white balance in your camera?

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

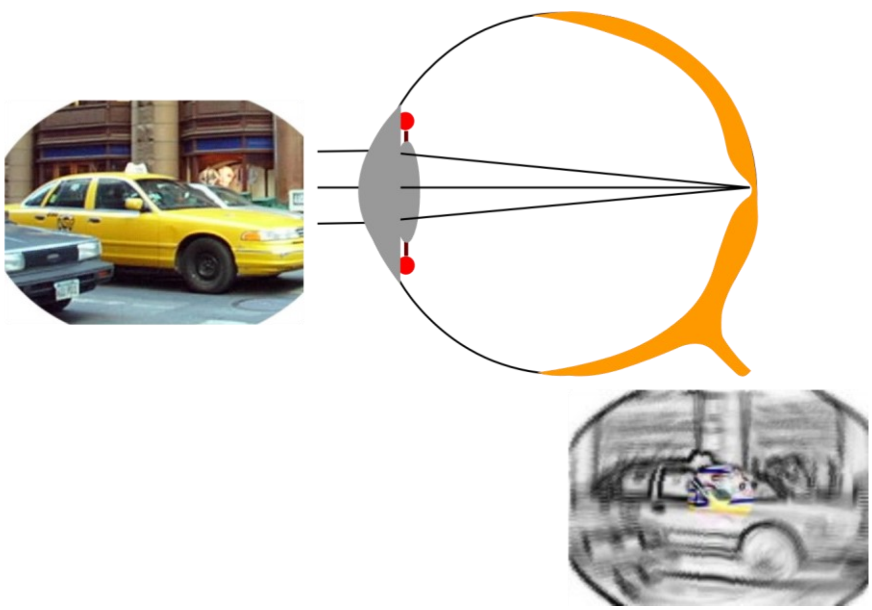


Figure 1.28 The Transformations from the Input to the Retina (top-left) to the Output of the Optic Nerve (bottom–right).

In Summary

The eye does three things.
1) It focuses the image clearly on the retina.
2) It detects light of various colors and intensities.
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 color 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

References

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