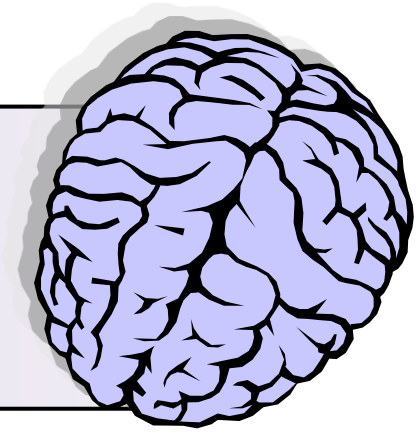
8. Systems neuroscience: How do we see?



Introduction

What does it mean, to see? The plain man's answer (and Aristotle's, too) would be, to know what is where by looking. [David Marr]

The magic of the human visual system are often lost on us because it is so naturally integrated with our daily experience and decision-making. So let's take a moment to be amazed: within 150 ms of the display of an image, your brain can encode whether there is an animal (or a car!) present. You can distinguish as few as six photons from noise. You can tell that there are two dots rather than one, 0.7 mm apart, from a distance of one meter. And if someone throws a ball at you as you *read this text*, you can bring your hand to the right place at the right time to catch it.

Another way to think of our visual system is that it has to solve an "inverse problem": objects reflect or emit light at various wavelengths, some of which hits our eyes. Our brain wants to recreate the arrangement and characteristics of those objects from the locations, intensities, and wavelengths of light received. All of this information travels through jus 1,000,000 fibers from the eye to the brain. For comparison, cell phone cameras hit 3MPix (3,000,000 pixels) in 2004.

As you would expect, "inverting" the transformation that gives rise to a retinal image is not theoretically feasible, even with infinite computational resources. But our goal is not to be perfectly correct or to we furnish constant proof of our percepts: it only matters, from evolution's standpoint, that we glean useful information about our surroundings. We need to know where there is food, where there are predators, who the people around us are and what moods they are in. And it turns out we get an astonishingly rich and *almost* always accurate percept by taking some computational "shortcuts."

Much of what we believe we "see" is, in fact, inferred rather than truly detected. In other words, we see with our brains. By seeking out and studying ways to trick the brain—the problems it gets wrong rather than right—we get a window into the mechanisms of human vision.

Senses and information

We can recognize a friend instantly—from his face, the back of his head, his voice, his walk, even his cough. We can distinguish millions of shades of color, as well as 10,000 smells. With no effort, we can feel a feather as it brushes our skin, and hear the faint rustle of a leaf.

Disregarding some philosophical quibbling, everything we know about the world comes to us through our senses. But what we perceive is quite different from the physical characteristics of the stimuli

around us. Our nervous system reacts only to a selected range of wavelengths, vibrations, or other properties. We cannot see light in the ultraviolet range, as bees can, and we cannot detect light in the infrared range, as rattlesnakes can. We are limited by our genes as well as our previous experience and our current state of attention.

The **sensory receptor** neurons in each sensory system (**Figure 1**) deal with different kinds of energy: electromagnetic (light), mechanical (sound and touch), or chemical (odors and flavors). They look different from one another, and they exhibit different receptor proteins. But each converts a stimulus from the environment into an electrochemical nerve impulse, which is the common language of the brain. This process is called **transduction**.

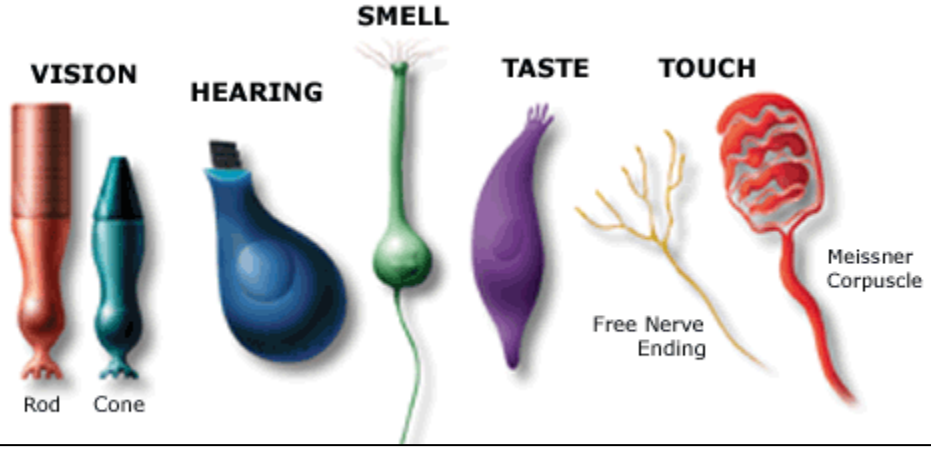


Figure 1. Various receptor cells for various sensations. Rod and cone cells of the retina are specialized to respond to the electromagnetic radiation of light. The ear's receptor neurons are topped by hair bundles that move in response to the vibrations of sound. Olfactory neurons at the back of the nose respond to odorant chemicals that bind to them. Taste receptor cells on the tongue and the back of the mouth respond to chemical substances that bind to them. Meissner's corpuscles are specialized for rapid response to touch, while free nerve endings bring sensations of pain. [*Illustration from http://www.hhmi.org]*

Once the information coming from the environment has been converted into nerve impulses, nearly all sensory signals first go to a relay station in the **thalamus**, which is a central structure in the brain. From the thalamus, the messages then travel to primary sensory areas in the cortex (a different area for each sense). There they are modified and sent on to "higher" regions of the brain, which integrate information coming from different senses as well as our prior knowledge.

The visual pathway

The visual system, which involves roughly a quarter of the cells in the human cerebral cortex, has attracted more research than all the other sensory systems combined. Not coincidentally, it is also the most accessible of our senses. Research on the visual system has taught scientists much of what they know about the brain, and it remains at the forefront of progress in the neurosciences.

Light rays reflected by an object (for example, a pencil as in **Figure 2**) enter the eye and pass through its lens. The lens projects an inverted image of the pencil onto the **retina** at the back of the eye. After photons hit neurons called **photoreceptors** in the retina, the signal is propagated through the **optic**

nerve to a major relay station in the thalamus, the LGN (**lateral geniculate nucleus**). Signals about particular elements of the pencil then travel to selected areas of the **primary visual cortex**, (also called V1), which curves around a deep fissure at the back of the brain. From there, signals fan out to "higher" areas of cortex that process more global aspects of the pencil such as its shape, color, or motion.

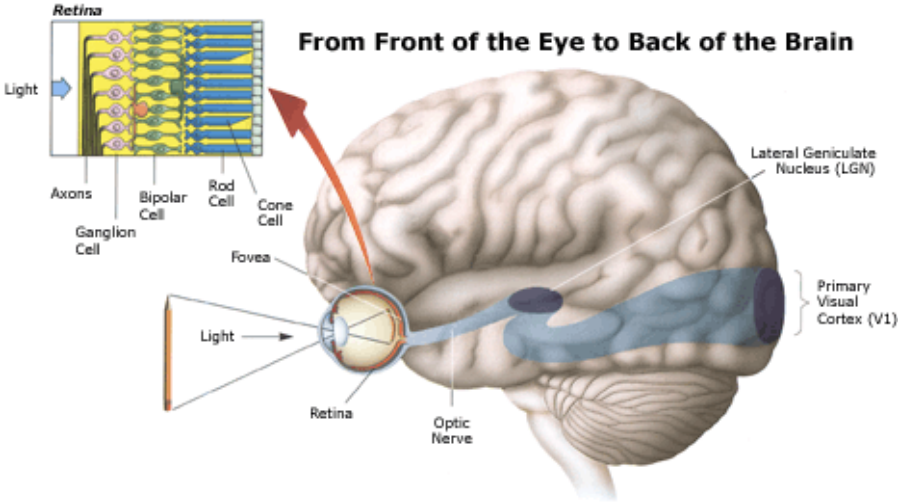


Figure 2. The 3 stages of the early visual pathway:
1. Retina (in the eye)
2. Lateral geniculate nucleus (in the thalamus)
3. Primary visual cortex (in the cerebral cortex).
[*Illustration from http://www.hhmi.org]*

The retina

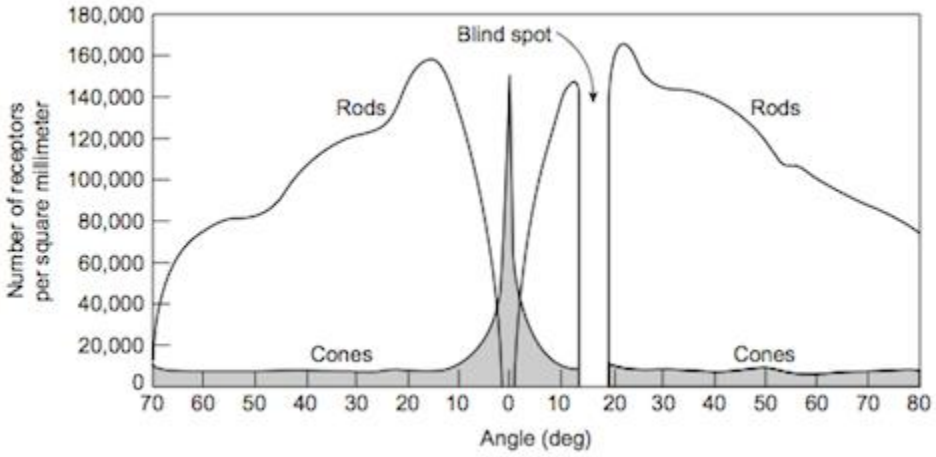
The retina, a sheet of neurons at the back of the eye, is the only part of the brain that is visible from outside the skull: any physician can see it using an ophthalmoscope. Photoreceptors, bipolar cells, and ganglion cells form the three layers of the retina. Surprisingly, the photoreceptors, which actually detect light, are at the very back of the retina—light has to go through the rest of the retina to reach them!

The 125 million photoreceptors in each human eye are neurons specialized to turn light into electrical signals. You might expect that light would cause these first cells in the pathway to fire action potentials, but instead they are tonically depolarized. In the dark, they constantly release the neurotransmitter glutamate. A photon within the right wavelength range can cause a conformational change in the pigment rhodopsin within a photoreceptor, which leads (via several more protein interactions) to hyperpolarization of the cell and an end to the glutamate release.

There are two forms of photoreceptors: rods and cones. **Rods** are about 100 times more sensitive to light than cones and do not convey color. When there is too much light, they become desensitized, so we only use them for vision in dim environments. **Cones** work in bright light and are responsible for acute detail and color vision. The human eye typically contains three types of cones, each sensitive to a different range of wavelengths. We estimate the spectrum of observed light by taking three measurements, each a different weighted sum of light intensity over visible wavelengths. The sensitivity of each type of cone (short, medium, and long wavelength) peaks at a different wavelength.

The numbers of rods and cones vary markedly over the surface of the retina (Figure ?). In the very center, we have only cones and they are very densely packed. This rod-free area is called the **fovea** and is about half a millimeter in diameter. Cones are present throughout the retina, but their density

decreases as we move away from the fovea. This means that we can see an object in detail only when looking directly at it. Objects in our peripheral vision are blurry because the density of photoreceptors on the edge of the retina is lower, and because signals from nearby rods are added together. We are very sensitive to movement at the periphery, but we can't distinguish details or fine structure without using the fovea (you can see that a person just entered the room while you are reading your book, but to know who she is you need to look at her – now you know why!).



Lindsay & Norman

Photoreceptors synapse on the bipolar cells layer, which in turn, communicates with the ganglion cell layer. Ganglion cells' axons pass across the surface of the retina, collect in a bundle at the **optic disc**, and leave the eye to form the **optic nerve**. This output of the retina is organized into two functional systems: one of them (called the parvocellular pathway) is very sensitive to color and image details. The other one (called the magnocellular pathway) is most sensitive to luminance changes and movement.

Because the optic nerve needs to leave the eye to get to the brain, there is a location in the back of the retina where there is no space for photoreceptors, and so the brain gets no information from the eye about this particular part of the world. This also has perceptual consequences: you have a "blind spot"! Have you ever noticed it? Check out **Figure 3**!

Figure 3. You have a blind spot! Close your left eye and stare at the cross mark in the diagram with your right eye. Off to the right you should be able to see the spot. Don't LOOK at it; just notice that it is there. Now slowly move toward your book and keep looking at the cross while you move. At a particular distance (probably a foot or so), the spot will disappear (it will reappear again if you move even closer). The spot disappears because it falls on the optic nerve head, which is the hole in the photoreceptor cell sheet where the axons of the retina leave the eye. *[Adapted from: http://serendip.brynmawr.edu]*

Receptive fields & retinotopic organization

The **receptive field** of a neuron is the area of the visual scene that can influence its response. In the retina, each neuron has a small window to the world: the neuron only receives signals from a small area of the visual field, and will not respond to changes in other parts of space.

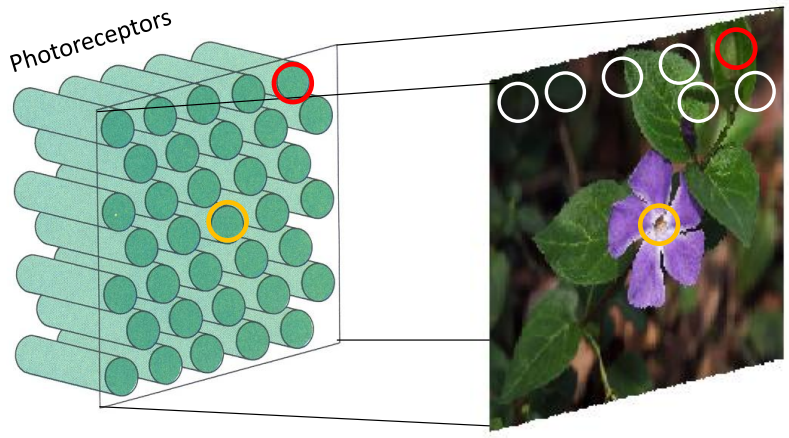


Figure 4. Receptive fields in the early visual system are retinotopically organized. The green cylinders on the left represent the photoreceptors in the retina and the small circles over the flower picture show the region of the images each photoreceptor "sees". *[Image adapted from: Hubel (1995): Eye, Brain and Vision]*

In the early stages of the visual pathway, through primary visual cortex, receptive fields are **retinotopically organized**. This means that neighboring neurons in your brain will respond to adjacent/neighboring regions in visual space (**Figure 4**). Receptive fields of photoreceptors are circular. The receptive fields of ganglion cells in the retina are also approximately circular, but they have two distinct concentric regions, called center and surround (**Figure 5**). ON-center receptive fields respond best to light falling on the center, and darkness falling on the surround; OFF-center receptive fields respond best to darkness on the center and light on the surround. Uniform illumination of the whole receptive field produces only weak responses (**Figure 6**).

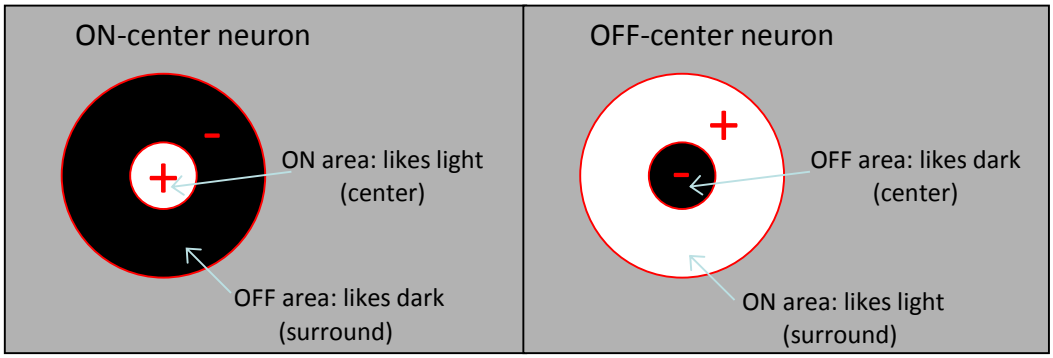


Figure 5. Concentric receptive fields of retinal ganglion neurons.

The map of the receptive field of a neuron is a powerful and convenient shorthand description of the neuron's behavior, and thus of its output. Understanding it can help us to understand why the cells in the intermediate stages are wired-up as they are, and will help explain the purpose of the pathways. Receptive-field maps are especially useful because they allow us to predict the behavior of a cell.

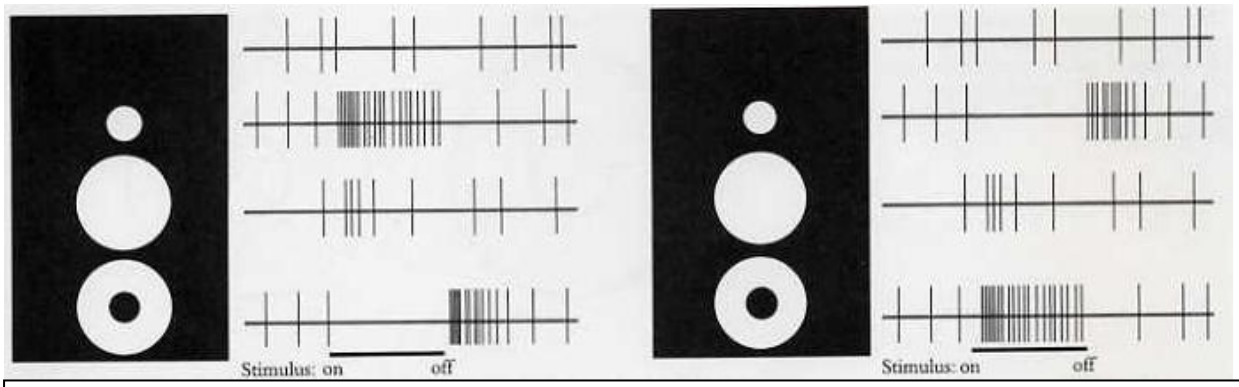


Figure 6. Ganglion cell responses.
Left panel: Four recordings from a typical ON-center retinal ganglion cell. Each vertical line represents an action potential (the unit of response of the neuron). To the left the stimuli are shown. In the resting state at the top, there is no stimulus: firing is slow and more or less random. The lower three records show responses to a small (optimum size) spot, a large spot covering the receptive-field center and surround, and a ring covering the surround only.
Right panel: Responses of an OFF-center retinal ganglion cell to the same set of stimuli shown at left
[Image from: Hubel (1995): Eye, Brain and Vision]

How are these center-surround receptive fields formed? **Figure 7** shows a possible circuit of how photoreceptors connect to retinal ganglion cells to give them their center-surround receptive field structure.

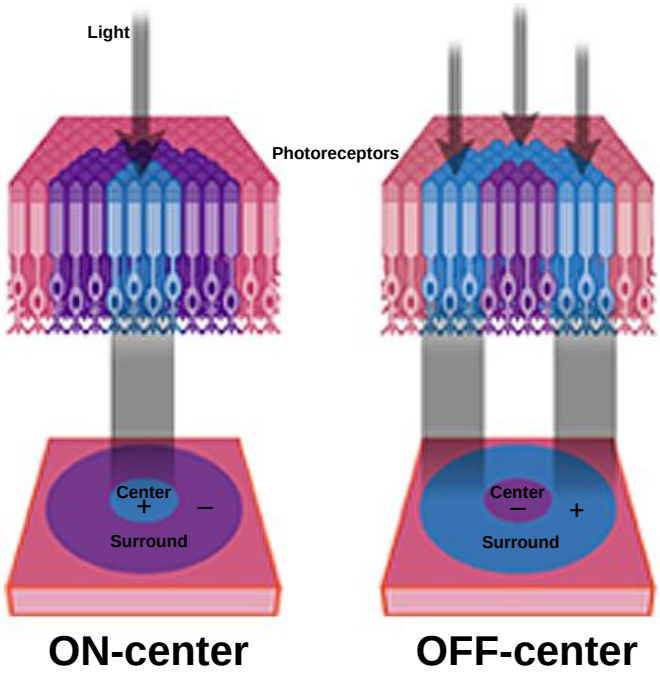


Figure 7. Possible circuit for center-surround receptive field formation. For ON-center neurons (left), some photoreceptors (in blue) have a positive connection with the center of the neuron, and the photoreceptors surrounding them (in purple) have a negative connection with the neuron. Photoreceptors further away (reddish), are not connected to the neuron, so the neuron "doesn't know" when there is light falling on them – we say that the light is outside of the receptive field of that particular neuron.

The LGN and primary visual cortex

The fibers coming to the brain from each eye pass uninterrupted through the **optic chiasm** (we saw this structure in the sheep brain dissection). There, about half the fibers cross to the other side of the brain. From the chiasm, most of the fibers continue to the two lateral geniculate nuclei (LGN) located in the thalami (see **Figure 2**). Because of the specific ways the fibers cross in the optic chiasm, each brain hemisphere will get information only from its **contralateral visual field**; that is: the left hemisphere gets information from the right half of your visual field and the right hemisphere gets information from the left part of your visual field (**Figure 8**).

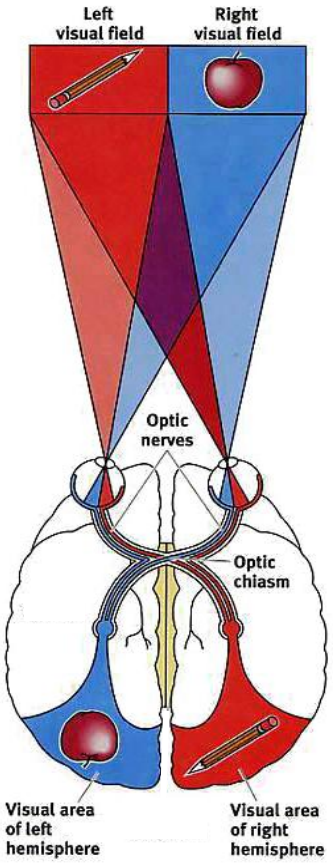


Figure 8. Left and right visual fields are represented in the contralateral hemisphere of the brain. *[Image from: http://rhsmpsychology.com]*

The LGN is often called a "relay station" because not much information processing takes place there: almost all of the roughly 1.5 million neurons in each LGN receive input directly from optic-nerve fibers, which is then projected to the cerebral cortex. Thus, the LGN is relaying the information it got from the eye directly to the cortex. Receptive fields in the LGN have the same center-surround structure as the ganglion cells in the retina and they are also retinotopically organized. Also as in the retina, neurons in the LGN are divided into two systems: one very sensitive to color and image details, and the other more sensitive to luminance changes and movement.

The axons from the LGN neurons leave the thalamus through the optic radiations and end in a region of the cortex at the back of the brain (occipital lobe) called the primary visual cortex, or area V1. V1 is

densely packed with cells and highly organized in 6 layers. In its middle layer, which receives input from the LGN, responses are similar to those observed in the retina and in the LGN (center-surround receptive fields). Neurons above and below this layer respond differently. They prefer stimuli in the shape of bars or edges at particular angles (orientation selectivity; see **Figure 9**).

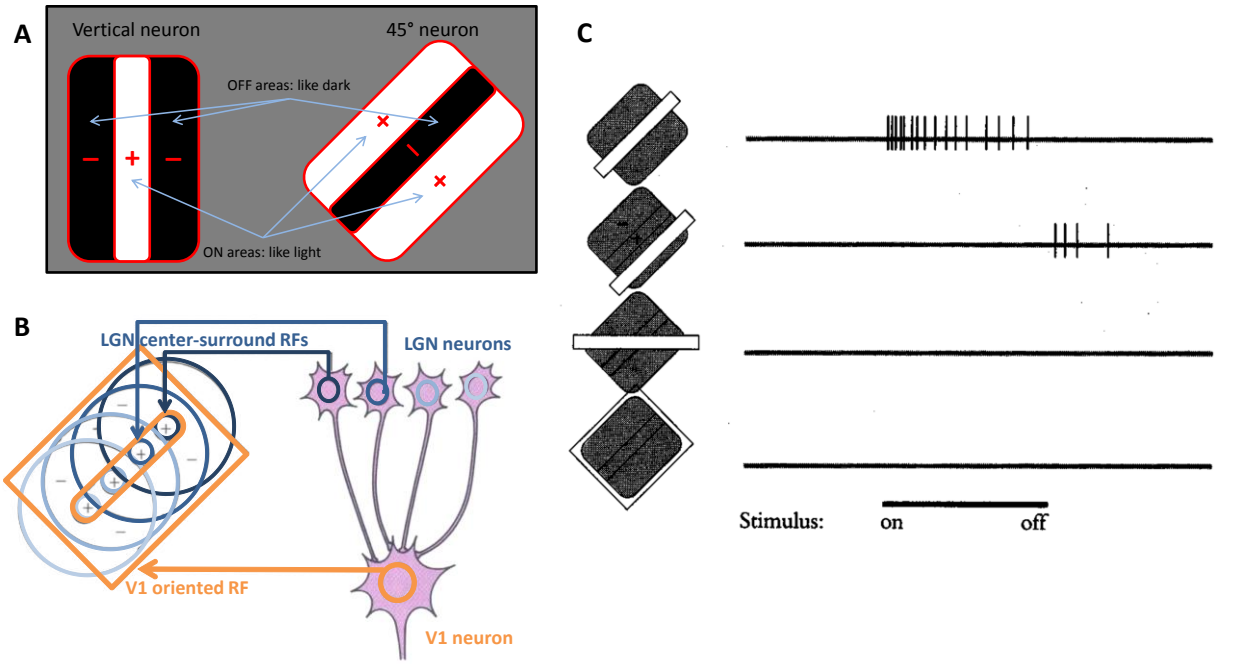


Figure 9. V1 receptive fields and responses.
(A) Schematic representation of the receptive field of a V1 neuron that only responds to bars of light at a specific orientation.
(B) Possible way of connecting several center-surround receptive fields to make an orientation selective receptive field: four adjacent neurons (right, in blue), each of them with a center-surround receptive field (left in blue), connect to one neuron (bottom, in orange) giving it an orientation selective receptive field (left, in orange).
(C) The stimulus line at the bottom indicates when the bar is turned on and, 1 second later, turned off. The top record shows the response to a bar of optimum size, position, and orientation. In the second record, the same bar covers only part of a negative area (no response while the bar is on). In the third record, the bar is oriented so as to cover only a small part of the positive region and a proportionally small part of the negative region; the cell fails to respond. In the bottom record, the whole receptive field is illuminated; again, there is no response.

Higher visual cortex

After V1, there are two main processing streams that are associated with different visual capabilities (**Figure 10**):

- The dorsal stream emphasizes motion analysis. After V1 and V2, the information flows to MT, MST and other intermediate areas. MT neurons have selective responses to the direction of stimulus motion, speed and depth differences. The highest stages of this stream are in the posterior parietal cortex. This stream is involved in assessment of spatial relationships and it is often called the "Where" pathway.

- The ventral stream emphasizes form and color analysis. After V1 and V2, the information flows to V4 and other intermediate areas; many V4 neurons have selective responses to stimulus color, orientation, width and length of bars, curvilinear and linear gratings, and contour features like angles and curves. The highest stages of this stream are in the inferotemporal cortex. This stream is concerned with visual recognition of objects and it is often called the "What" pathway.

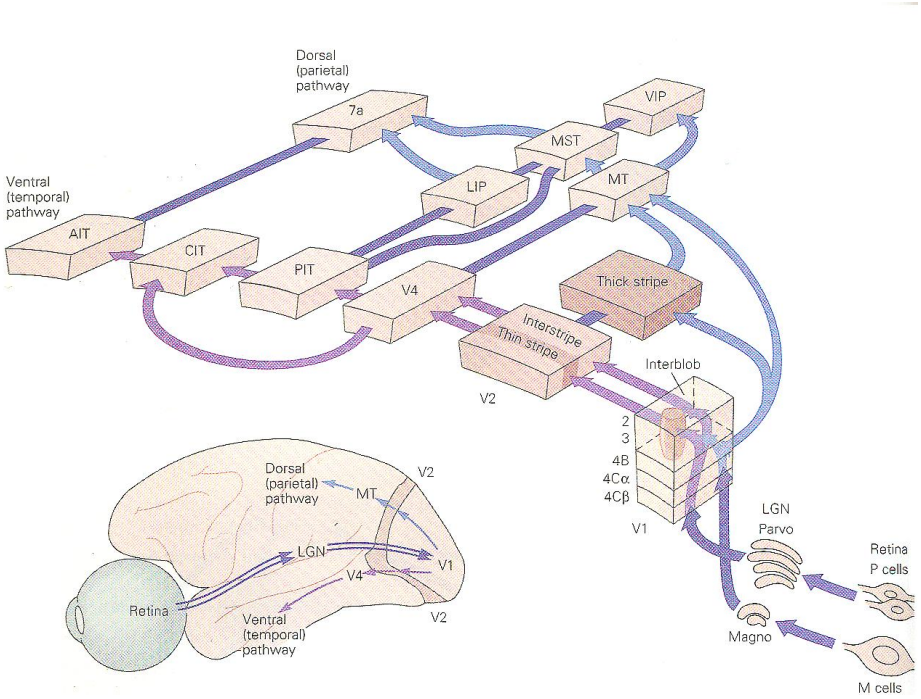


Figure 10. Schematic of the two visual pathways (dorsal-where and ventral-what) in the primate brain. *[Illustration from Kandel et al., 2000]*

Neural adaptation

Our senses are finely attuned to change. Stationary or unchanging objects are mostly unseen, but your attention is immediately drawn to a spider crawling across the ceiling. You could sleep next to a waterfall, but the sudden hiss of Caltech's sprinkler system may wake you up. The feel of a sweater against our skin is soon ignored, but when an insect lands on your leg touch receptors on the fire a message that travels through your spinal column to alert your brain, and the signal leads you to swat the insect at just the right place.

Animal nervous systems have evolved to detect changes in the environment because spotting differences promotes survival. **Neural adaptation** takes place in all of the senses, including touch. For instance, you may feel your shoes when you first put them on in the morning, but the feeling goes away after a while. You probably do not want to be aware of your shoes 16 hours a day. If you wiggle your toes, however, you can feel your shoes again. So if a stimulus does not change, neurons "adapt" and stop responding to it. This reduces the amount of information the brain needs to process.

Frogs demonstrate extreme visual adaptation: they cannot see static objects. Exposed to an unchanging stimulus, visual neurons in the frog brain adjust their action potential output such that they gradually stop firing. Neural adaptation saves energy, but also limits sensory perception. Human neurons also adapt to sameness, but human eyes create their own motion: even when you fixate on a specific point, your eyes never stop moving. These "fixational eye movements" constantly move the image on the retina (like when you wiggle your toes to notice your shoes) so that your perception of objects never goes away--as happens to the frog. Yet if you could somehow halt these miniature motions while fixing your gaze, a static scene would fade from view!

Adaptation can occur at many levels within visual processing, from the retina (leading to afterimages) to higher visual areas. This causes effects analogous to retinal afterimages for motion and even face processing, as we will explore in class tomorrow.

Chapter Resources

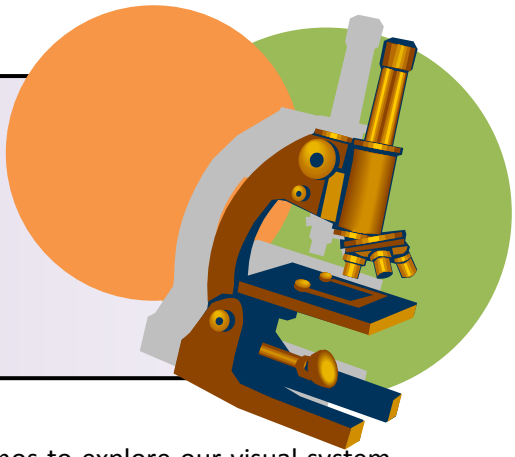
Vocabulary

Sensory receptor
Transduction
Retina
Thalamus
Lateral geniculate nucleus
Primary visual cortex
Photoreceptors (Rods & Cones)
Fovea
Optic nerve
Receptive field
Retinotopic organization
Optic chiasm
Neural adaptation

Web links

- David Hubel's book: "Eye, Brain and Vision"
  http://hubel.med.harvard.edu/book/bcontex.htm
- Howard Hughes Medical Institute's page on the brain & the senses:
  http://www.hhmi.org/senses/
- Best Illusion of the Year Contest
  http://illusioncontest.neuralcorrelate.com/
- Michael Bach's interactive page on visual illusions
  http://www.michaelbach.de/ot/

LAB 8: Visual illusions



Today instead of a lab we will develop several class activities and demos to explore our visual system. You will need to document your observations and fill in answers as we go through the activities.

Visual acuity test

1) Where is your vision better, in the center or in the periphery?

2) What is the physiological reason?

Blind spot mapping

3) What is the blind spot?

4) How big is it?

5) Describe what you did to map it.

Hubel & Wiesel video

6) What were Hubel and Wiesel trying to do in this video?

7) Why were they using a bar of light instead of a flash light as we did in our RF mapping exercise?

Attentional & change blindness

8) Why isn't change blindness a major problem in everyday life? How would you reassure yourself that you aren't missing changes like the ones we just saw?

Fading demo

9) Describe what happened in this illusion

10) Why don't objects usually fade from your view? Give an example of sensations that do fade in other modalities.

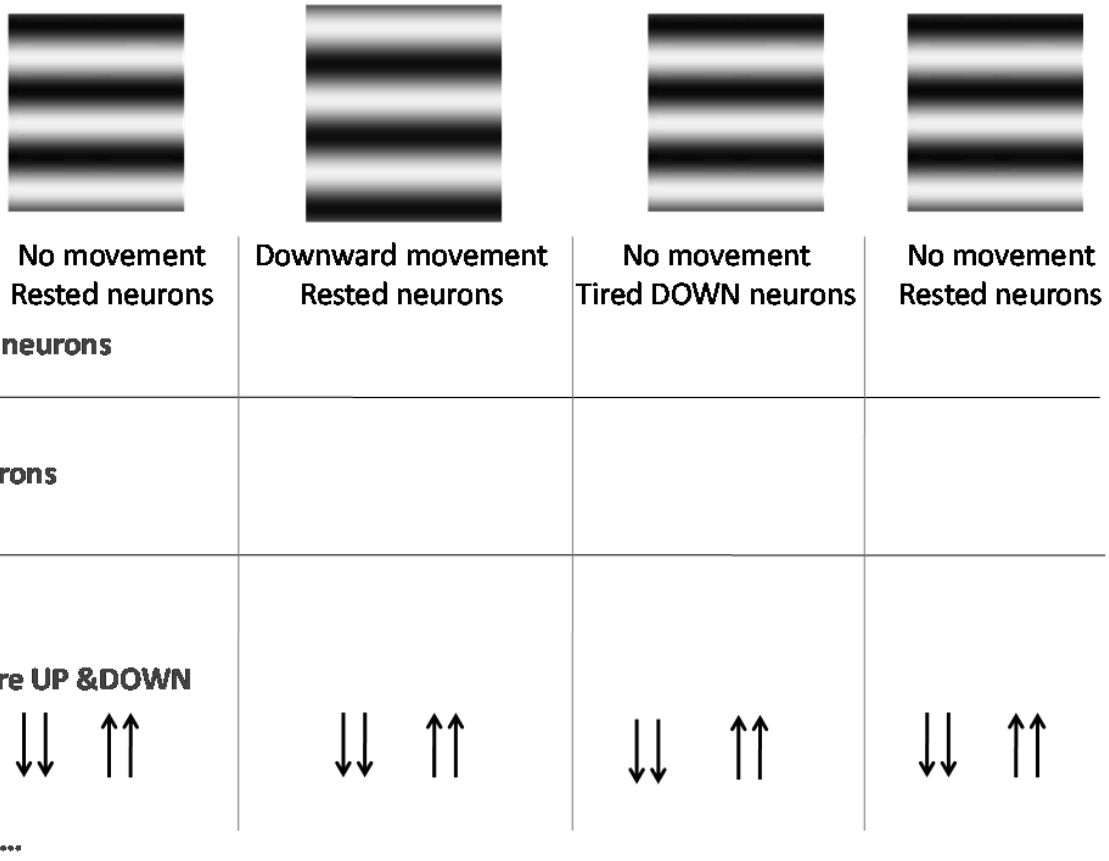
Observe & describe a visual illusion

1) Describe the illusion that was assigned to your group.

2) How did it "fool" your visual system?

Adaptation & afterimages

Fill in the following charts as we go through the activity. Each line vertical line that we draw will represent an action potential.



No movement Rested neurons	Contraction Rested neurons	No movement Tired CONTRACT neurons	No movement Rested neurons

CONTRACT neurons

EXPAND neurons

Compare CONTRACT & EXPAND

We see…

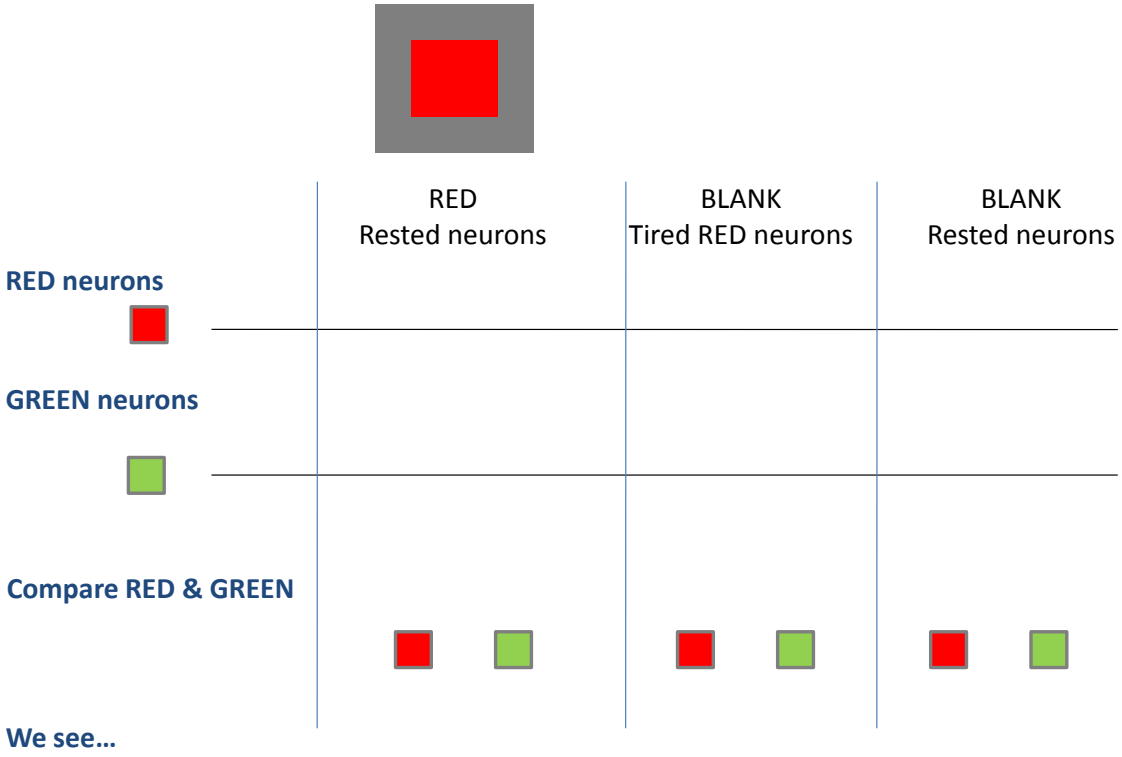
Gray Rested neurons	Bright Rested neurons	Gray Tired BRIGHT neurons	Gray Rested neurons

BRIGHT neurons

DARK neurons

Compare BRIGHT & DARK

We see…


RED
Rested neurons
BLANK
Tired RED neurons
BLANK
Rested neurons
RED neurons
GREEN neurons
Compare RED & GREEN
We see…

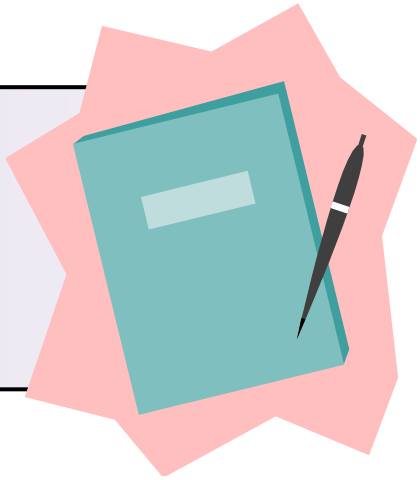
Binocular rivalry

11) Why doesn't binocular rivalry typically occur?

12) Record your dominance times in seconds:

Image 1	Image 2

Visual illusions homework



1. Report the average dominance times you recorded for each of the two images.

2. Early visual scientists thought that a large bright light would best activate retinal ganglion cells – why were they wrong?

3. Draw the stimulus that would maximally activate an OFF-center retinal ganglion cell.

4. We saw in our visual acuity demo that our vision is much worse in the periphery than in the fovea. Explain why. If our peripheral vision is so bad, why don't objects around you look blurry?

5. In the "Attentional & Change Blindness" video we saw that it is possible to miss things that we would have thought were impossible to miss. Give a "real life" example of a problem attentional blindness could cause. Think of a situation where not being aware of how "blind" we can be could be an issue.

6. Why don't blindness within the blind spot and during blinking/saccades make us vulnerable or confused in everyday life?

7. Pick a visual illusion (from the websites in the reading) and answer the following questions:
    a. Describe the illusion and how it fools our visual system.
    b. What changes to our visual system would let us perceive the illusion "correctly"? Is there any benefit to our actual vulnerability to the illusion?
    c. If you had to design an experiment to understand how this illusion works, what would you vary in your tests? Why?