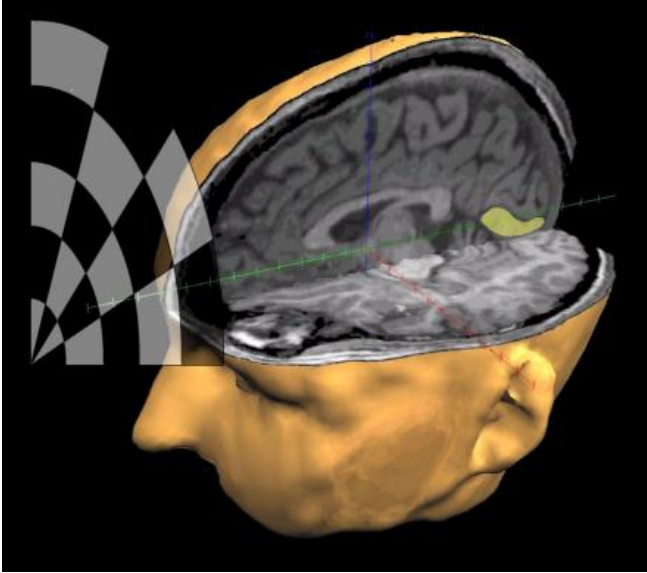


The Visual Cortex



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Introduction

The diagram here shows that visual stimuli activate a structure called the primary visual cortex. The activation is in a fold in the cortex called the calcarine sulcus.

This activation, on the right side of the brain, only occurs when a visual stimulus appears on the subject's left.

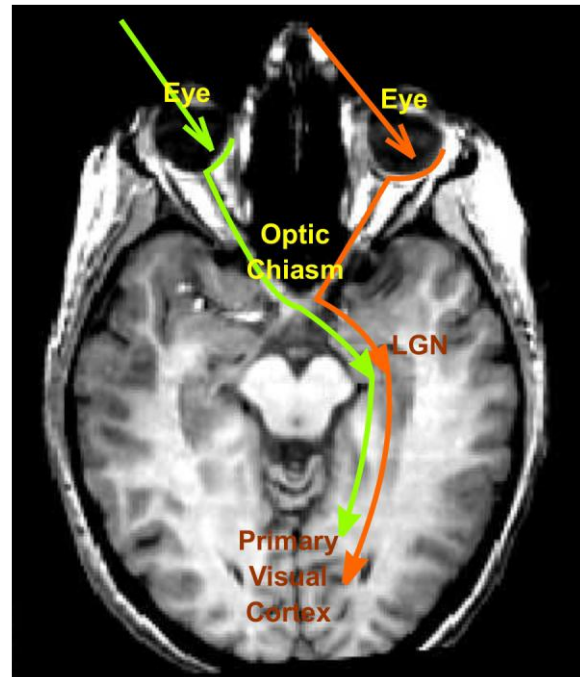
In this session we will learn

- 1) **how** the signals from the eye reach the primary visual cortex,
- 2) **what** cells in this area do with the signals they receive from the eye, and
- 3) **where** signals go from here.

Optic chiasm

Images seen on one side are processed by the opposite side of the brain.

To do this, the ganglion cells on the medial side of each eye, (from the middle of the fovea on, shown in green) cross at the **optic chiasm**.



Before reaching the primary visual cortex, fibers of the optic nerve make a synapse in a part of the thalamus called the **lateral geniculate nucleus (LGN)**.

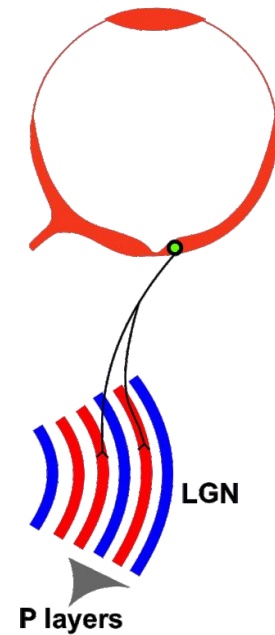
Here information from each eye does not mix. It remains separate until the primary visual cortex

Where do the eye's ganglion cells project to?

The **LGN** is composed of 6 layers; 3 receive information from one eye and 3 from the other.

Ganglion cells from the fovea project to layers composed of small cells called the **parvocellular (P)** layers.

These provide the fine details required to determine **what** an object is.



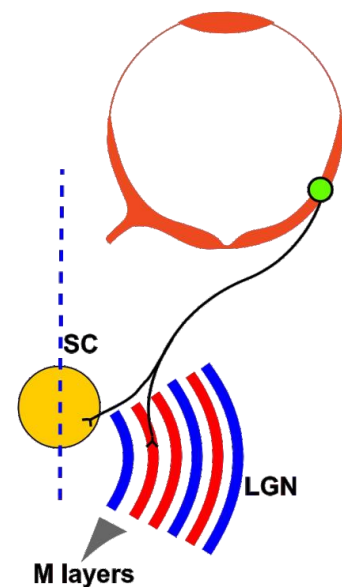
Ganglion cells from the peripheral retina project to the **magnocellular (M)** layers.

These provide only coarse information as to **where** something is. This is insufficient to determine what an object is.

These ganglion cells also project to several structures in the brainstem, including the **superior colliculus (SC)**.

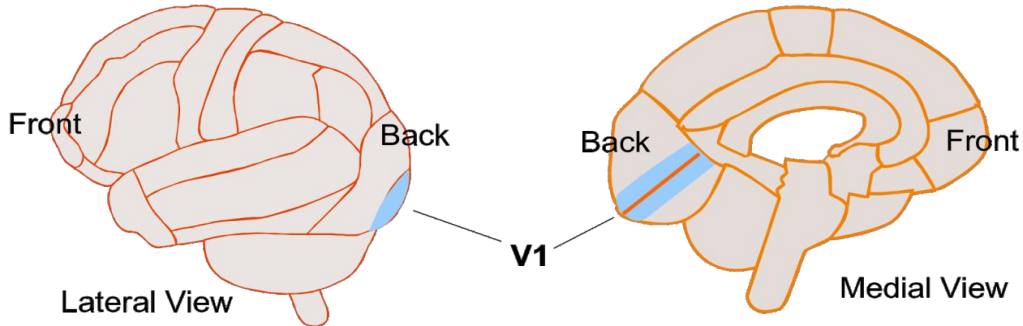
The SC causes the eye and head to turn to the location of a visual object that draws your attention: the "**visual grasp reflex**".

This in turn places the object's image on the fovea and activates P cells. These then provide the detailed information required by the visual cortical areas to determine what the object is.



To where do LGN neurons project?

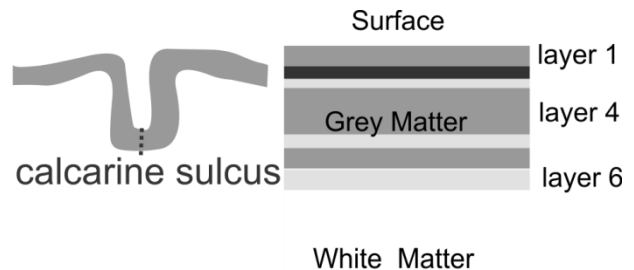
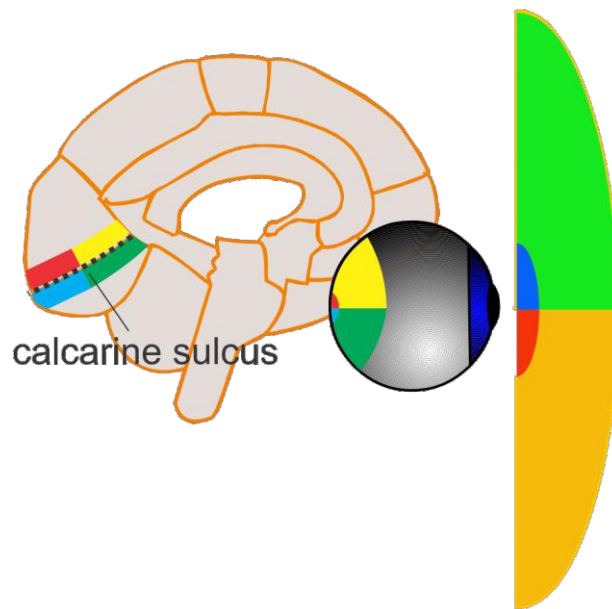
LGN neurons project to the **primary visual cortex**, which is located at the back of the head mostly on the medial side. The primary visual cortex has many names: V1, area 17, & striate cortex.



The primary visual cortex lies in the fold of the **calcarine sulcus**. The fovea is represented at the posterior end of the calcarine sulcus. This small part of the retina has an expanded representation, which occupies about half of the primary visual cortex. The remaining peripheral retina is represented at the anterior half. Things above the line of sight are represented on the lower half of the calcarine sulcus. The lower visual field is represented on the upper half of the calcarine.

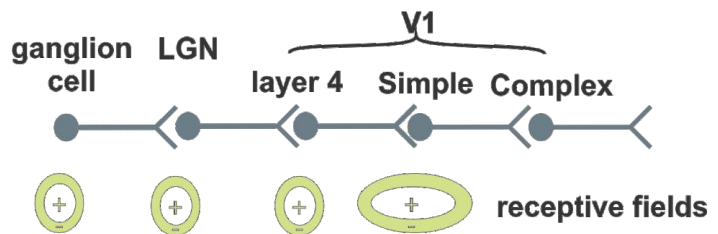
V1, like every cortical area, is made up of a thin sheet of grey matter near the surface. To pack lots of grey matter into a skull, this sheet is folded. Having lots of grey matter is good because this is where the cells and connections are. The connections are our memory store. Below the grey matter lies the white matter. White matter contains the nerve fibers; the "wiring" that interconnects cells.

The gray matter has 6 layers. V1 is also called the striate cortex because of a very **thick layer 4**. This is where massive input from the LGN ends.



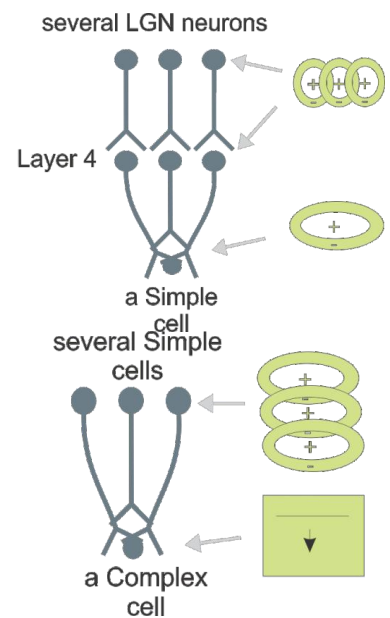
Primary visual cortex (V1) contains 3 cell types

1. **Layer 4 cells**, whose receptive fields are round like those of LGN and ganglion cells,
2. **simple cells** with elongated receptive fields and thus maximally activated by a line of a particular orientation, and
3. **complex cells** whose receptive fields are similar to those of simple cells except that the line can lie over a larger area of the retina and these fire more to moving lines.



How are simple and complex receptive fields produced?

Several ganglion cells, whose receptive fields lie along a common line, converge by way of the LGN onto a simple cell. The one shown here fires maximally for a horizontal line and minimally for a vertical line. Each simple cell is selective for one particular orientation.



Complex cells: Several simple cells of the same orientation converge onto a complex cell.

Why is this important and clinically relevant?

These studies show how the visual system can construct complex representations from simple features.

The receptive field of a simple cell is tuned to a very particular stimulus. The complex cell generalizes this particular stimulus over a larger area.

We will see that, further in the visual stream, one finds cells that respond only to particular faces that are generalized over the whole retina.

The discovery of simple and complex cells is the work of David Hubel, a medical student from McGill, who grew up in Windsor, Canada and who together with Torsten Wiesel, was awarded the 1981 Nobel Prize in Physiology or Medicine. They showed how changes in the organization of these cells can lead to a form of blindness called amblyopia.



David Hubel

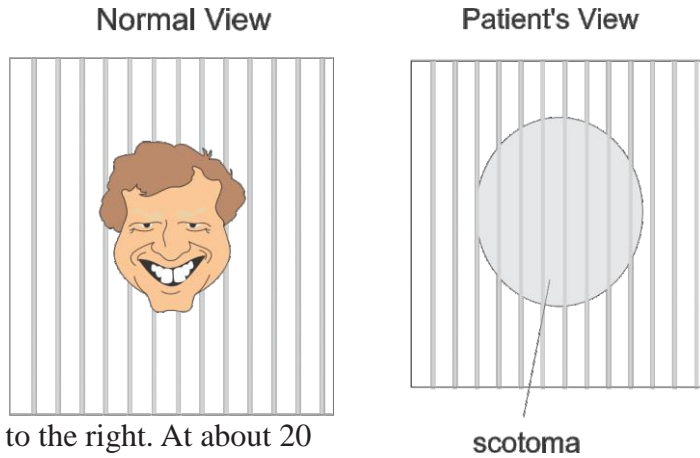
What patients with a scotoma (blind area) on their fovea experience?

When viewing a face against a striped background, patients do not see the face (because it is in their blind area) but see stripes where the face should be.

This "filling in" is produced by cortical simple and complex cells.

These cells are producing a similar filling in now as you read this. You have a blind spot on your retina but are not aware of a black area on this page. The blind spot is where the optic nerve leaves the back of the eye.

To find your blind spot, close your left eye and look at some object on a blank wall. Hold a pencil, preferably with a red tip, at arm's length and at eye level. Move the pencil to the right. At about 20 degrees to the right the tip should disappear. Now raise the pencil. The tip of the pencil should reappear and there is no empty gap in the pencil where the blind spot was. Your visual system fills in the image of the pencil.



You can also look at the red x below while paying attention to the dot on the right. It may be difficult at first to keep from taking a peek at the dot. Remember to close your left eye.

- In the first row, when you move the page to between 1 and 2 feet away from you, the dot should disappear.



- In the second row, the gap in the line should disappear.



- In the third, the face should disappear but the lines should be visible where the face was. You should see what the patient with the scotoma in the retina saw.



Describe the structure of primary visual cortex (V1).

V1 is a map of the retina composed of a grid (1 mm by 1mm) of **hypercolumns**.

- Each hypercolumn analyses information from one small region of retina.
- Adjacent hypercolumns analyze information from adjacent areas of retina.
- The map is distorted. The fovea is over-represented. The area devoted to the fovea is about the same as that devoted to the rest of the retina.

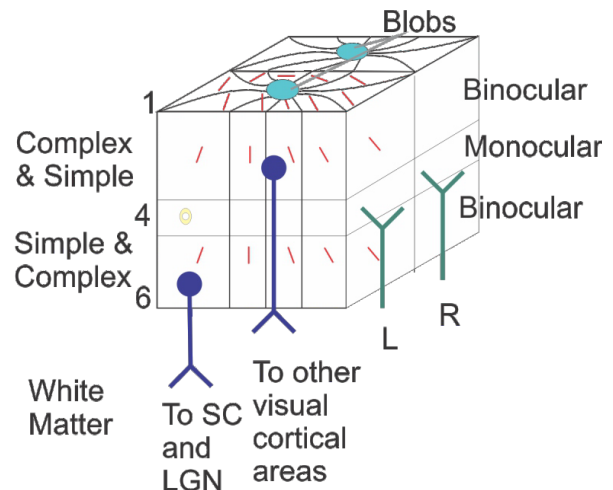
Input from the left and right eyes (via the LGN) enters at layer 4. Here one finds cells driven by input from one eye or the other but not both (**monocular cells**).

Information from the two eyes **first** comes together in **binocular** simple and complex cells located above and below layer 4. These cells are important because they contribute to the sense of **visual depth**.

The columnar organization of the primary visual cortex

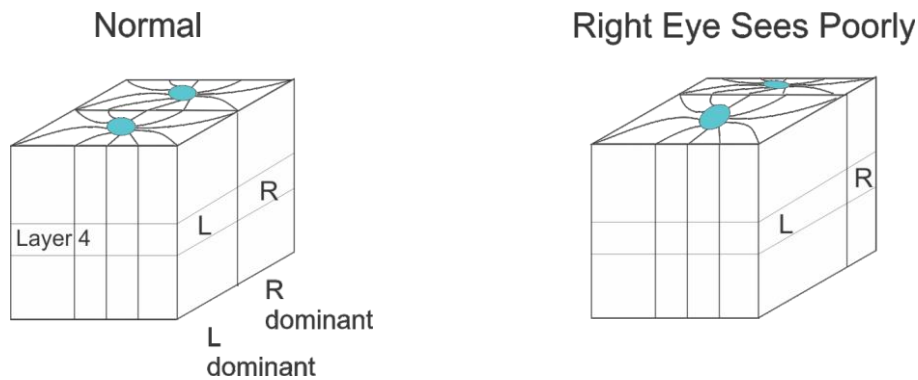
Each hypercolumn extracts the following features:

- **Stereopsis:** In each half, one or the other eye dominates. One sees in depth by combining information from the two eyes in binocular cells located above and below the input layer 4.
- **Colour:** In the center of each cube one finds a column, called a blob, which contains color sensitive double opponent cells.
- **Orientation of line segments:** Radiating from the blobs, like spokes from the center of a wheel, one finds simple and complex cells ordered into pin wheel segments of the same orientation. The preferred orientation changes gradually as one goes around the pin wheel.



Influence of early development on the structure of visual cortex

What is the effect of early visual deprivation in one eye?



In a normal adult, one side of the column becomes dominated by the right eye and the other by the left eye.

In an infant, the two eyes compete for representation. If one eye sees poorly, the good eye takes over the cortical representation of the bad eye. In the extreme case, the bad eye loses all its representation and become permanently blind. This is called **amblyopia** (cortical blindness). The infant remains blind in one eye even if the function of that eye is restored to normal.

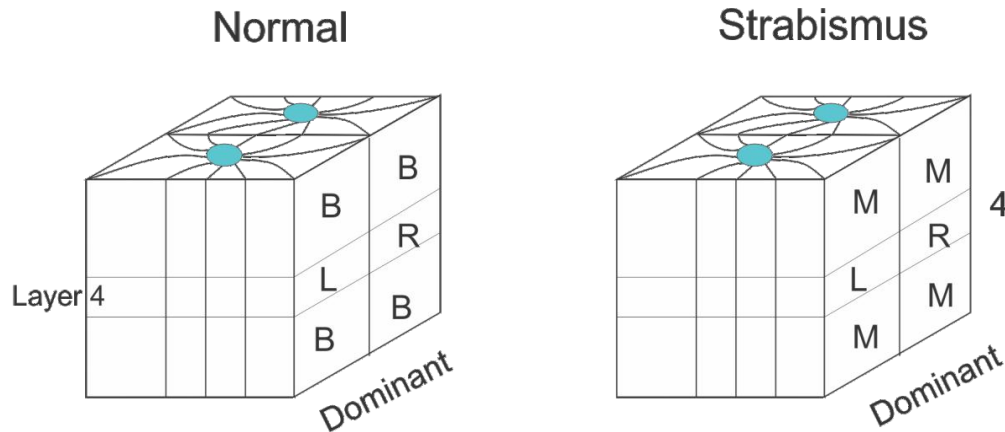
Critical period: The visual cortex is particularly sensitive to deprivation (plastic) in the first year of life. A cataract at birth, which is not removed for a year, has a permanent effect.

A similar deprivation in an adult has little effect. When a cataract develops in old age, vision is restored as soon as the cataract is removed.

This early sensitivity to competition in infants is called the **critical period**.

What is the effect of early strabismus?

In early strabismus the two eyes are normal but do not align on the same visual target.



In the normal cortex, cells above and below layer 4 are binocularly driven.

These cells are important for **stereopsis** (the visual sense of depth).

In an infant with prolonged strabismus, each eye is stimulated and thus retains its representation in visual cortex. However binocular cells are never activated simultaneously by the same stimuli. These cells become monocularly driven and the child permanently loses **stereopsis**.

Because strabismus causes double vision, the image from one eye may be suppressed. This suppression may lead to amblyopia.

What are the synaptic mechanisms for this plasticity?

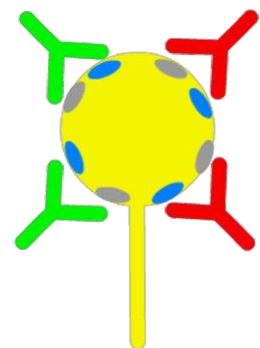
The basis of this plasticity is synchronous activity: The key is the NMDA receptor (colored in blue) which opens only when the cell is strongly depolarized. If two synapses fire synchronously, they strengthen each other at the expense of others that fire asynchronously. Cells that fire together wire together. This model has been used as a basis for plasticity or learning throughout the brain.

When visual inputs from the left eye are synchronous, but that from the right is asynchronous, the left eye's synapses become stronger and it takes over.

If all inputs are synchronous, both eyes' synapses become stronger and both eyes remain represented. Some postsynaptic changes are rapid but not long lasting while others take days and are semi-permanent.

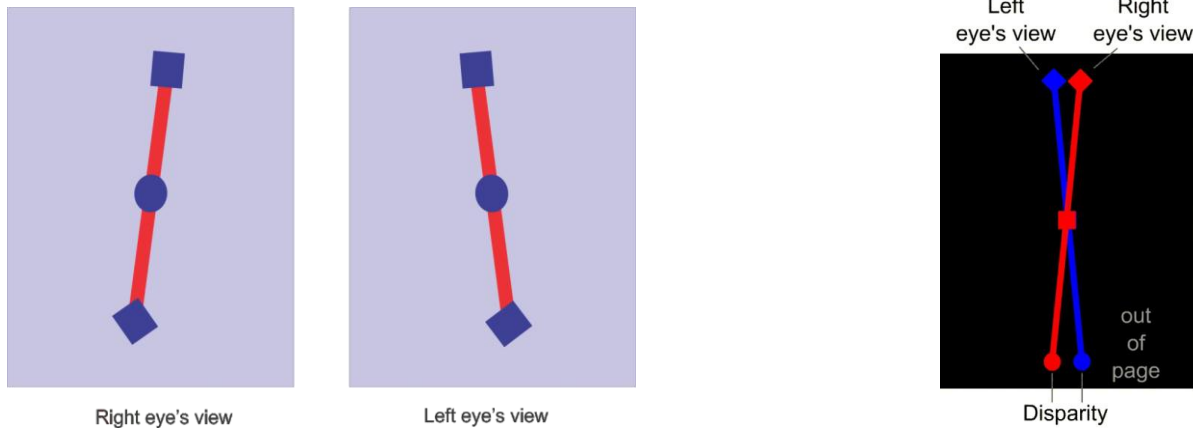
Summary

Sensory experience influences how the brain wires itself. A child's early visual experience is crucial for normal development.



Why are two eyes better than one?

When you look at the center of a real vertical bar whose top is leaning away from you, the images seen by the two eyes are different. The top of the bar leans to the right in the right eye and to the left in the left eye. This difference is called **disparity**. Binocular cells, above and below layer 4, are tuned to this disparity. To activate these cells, converge your eyes while looking at the figure below. At some point you should see three images not just two. When this happens, the bottom of the line seems to be coming out of the page. This is **stereopsis**.



This is what the visual cortex sees when the images of the two eyes are combined. The bottom of the line appears in different places on the two eyes. This difference is called disparity and gives the illusion of depth.

How do binocular cells signal disparity?

Each binocular cell in V1 is best activated by a **particular retinal disparity**.

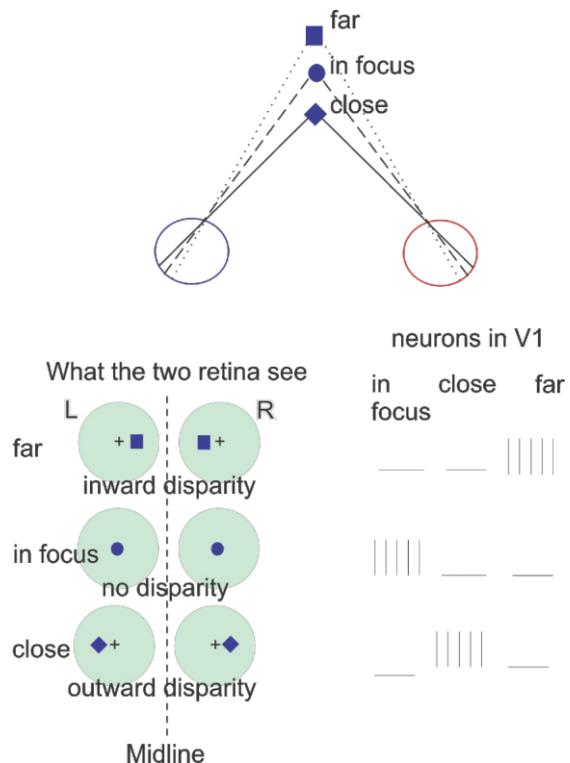
Below is the activity of three such cells. Activation of cells like these gives one a sense of depth (near or far).

Collectively they give images their **3 dimensional appearance**.

The 'far' neuron is best activated (vertical lines) with an inward disparity. The images are displaced in a nasal direction in the two eyes.

The 'in focus' cell is activated when there is no retinal disparity. The images are centered on the fovea of both eyes.

The 'close' neuron is best activated with an outward disparity. The images are displaced in a temporal direction in the two retinas.

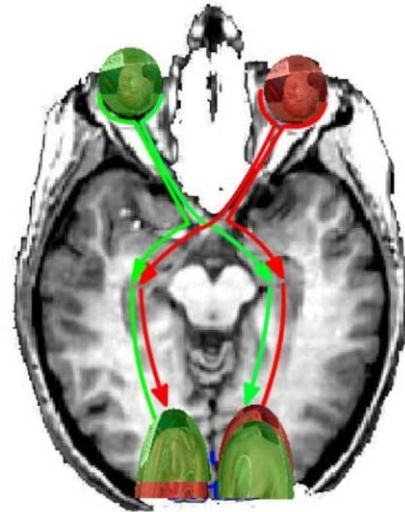


In summary

The eye flips the image of the world.

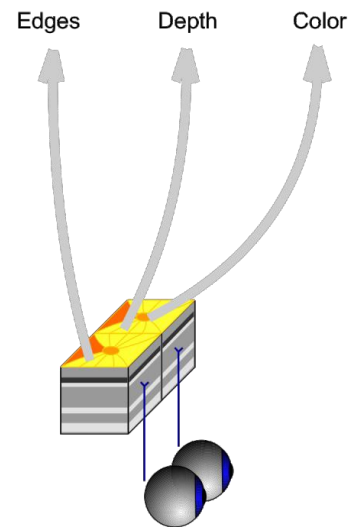
The retina, by magnifying the image that falls on the fovea, distorts this image.

The images from the two eyes are combined in the primary visual cortex. The left cortex codes images seen on one's right side (by both eyes). By comparing these two images, depth is computed.




The primary visual cortex separates the image into distinct **feature channels**. Different groups of cells work collectively to extract each feature.

- 1) Cells in the blobs extract **colour**.
- 2) Binocular cells compute the retinal disparity and thus **depth**.
- 3) Simple and complex cells are activated by **edges** of particular orientations.



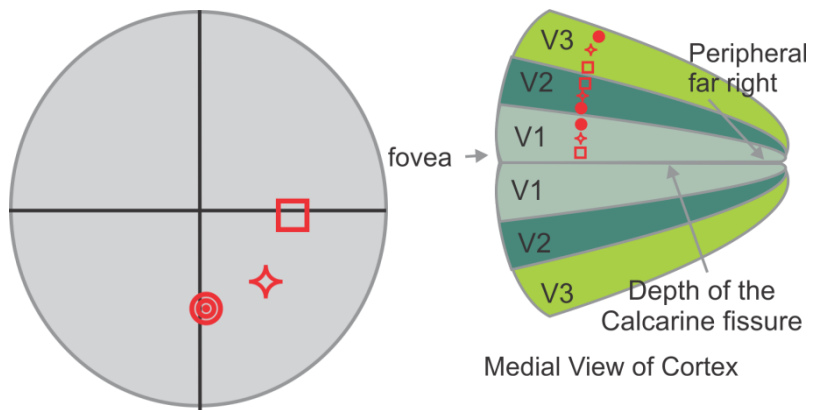
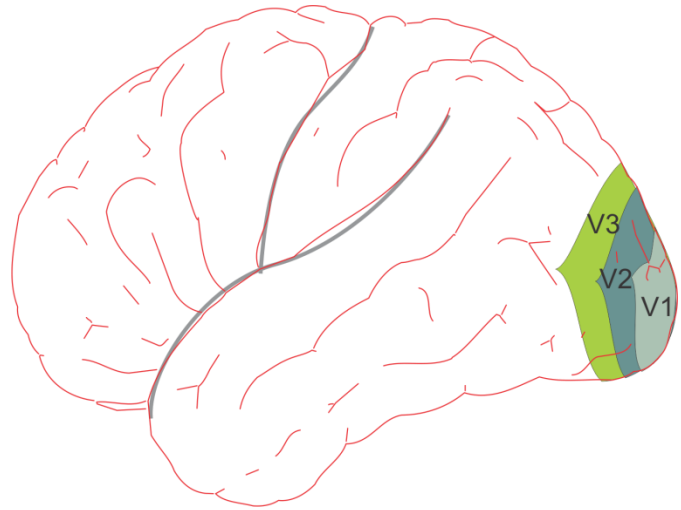
Where does visual information go to after primary visual cortex?

From the primary visual cortex information is sent to V2 and then to V3.

In each map, the retina is re-represented. Note that the  is seen in the right lower visual field and is represented in the left upper visual cortex. It is represented 3 times, once in each area: V1, V2, and V3.

Each map is a mirror image of the preceding.

As we will see in later sections other sensory cortical areas (e.g. touch) also have multiple representations with the mirror property.



Where does visual information go next?

From V3, information diverges to over 3 dozen higher order visual areas.

Each processes some special aspect of visual information. These visual areas are like a multi-screen cinema. The main difference is that each screen is showing a different attribute of the same movie; some just the motion, others the colors, etc.

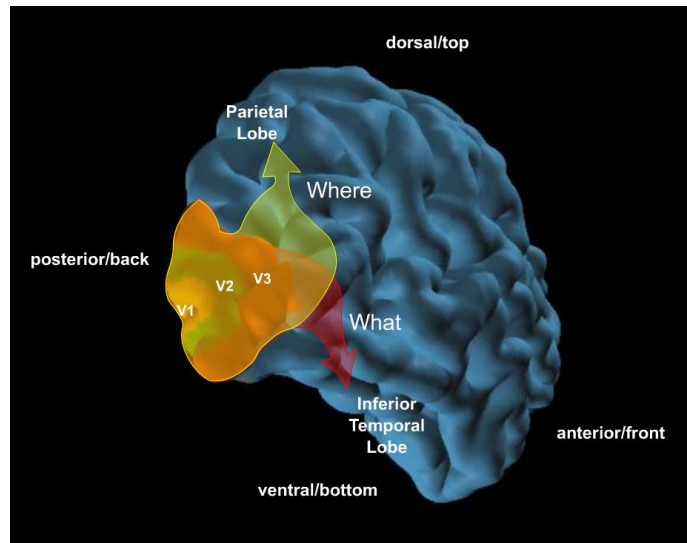
Information flows along two main streams.

1) The dorsal stream, to the intra parietal sulcus in the parietal lobe, is concerned with selecting actions to particular spatial locations. For this reason it is called the "**where**" stream.

2) The ventral stream, to the inferior part of the temporal lobe, is concerned with the perception and recognition of objects, e.g. faces. This is called the "**what**" stream.

Lesions in the "what" stream produce deficits in object recognition: visual agnosia. Patients can reach for objects but cannot say what they are.

Patients with lesions in the parietal lobe can exhibit optic ataxia. They can recognize objects but fail to reach for them accurately.



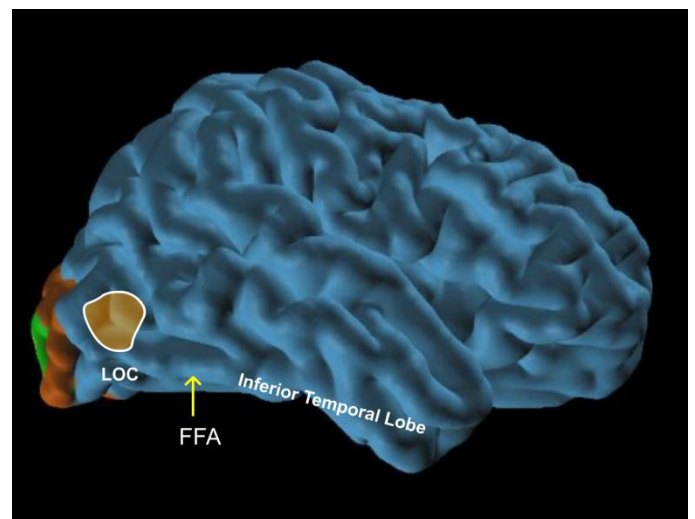
What is the function of the inferior temporal cortex (IT)?

The **lateral occipital complex** (area LOC) is an important way station along the ventral stream. LOC codes that something is an object part while areas of the inferior temporal cortex code a particular object (e.g. a face).

Lesions of LOC result in **visual agnosia**, the inability to perceive objects through vision.

Patients can see the object's form and even copy it but cannot tell what that object is or how to use it. They cannot distinguish between a knife and a fork by vision but can do so by touch.

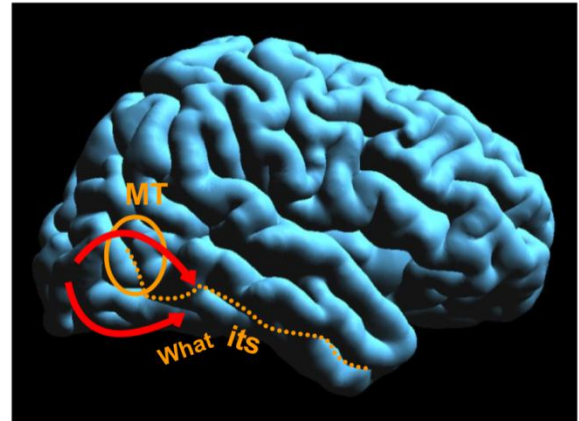
Patients with lesions in the **inferior temporal lobe (IT)** cannot recognize particular classes of objects. For example patients with lesions of the right **Fusiform Face Area (FFA)** cannot recognize friends (or even themselves in a mirror) from visual clues (**prosopagnosia**). They are able to recognize people through other visual cues such as gait or other modalities such as the voice. They can also recognize features that make up a face such as eyebrows, lips etc.



The visual perception of motion

The cerebral cortex has several regions that specialize in analyzing visual motion. One of the most prominent is the **middle temporal motion area** (MT), a part of the dorsal stream.

Without area MT our automatic perception of motion is lost. Instead the visual motion becomes a series of stills. Simple judgement of an object's speed and direction becomes difficult.



Neurons in area MT have large receptive fields, roughly ten times larger than those in V1. For this reason area MT has poor visual acuity.

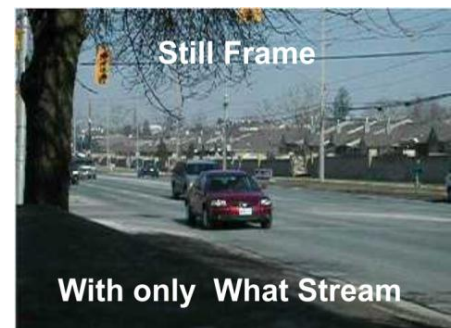
Also area MT sees only in black and white, not in color. Thus while MT is excellent at determining the direction in which an object is moving, it cannot identify the object.



Inspecting the detailed features within an object is the function of the ventral 'what' stream.

But the 'what' stream has a poor sense of motion.

With both streams one can perceive **what** an object is and **where** it is going.



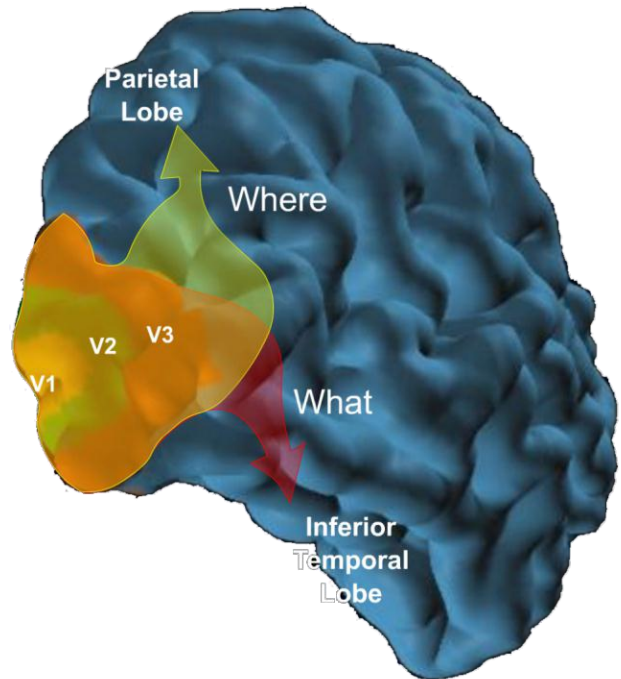
Summary

Visual information from V1 divides along two streams:

- 1) a dorsal “Where” stream: concerned with the spatial relationship between objects and
- 2) a ventral “What” stream: concerned with object recognition.

The ‘What’ stream sees in detail because it gets most of its input from P ganglion cells in the fovea.

The ‘Where’ stream gets less detailed input from M ganglion cell in the peripheral retina and excels at coding the locations of objects around us.



Practice problems

1. Strabismus in early childhood will produce
 - a) a loss of orientation columns in primary visual cortex (V1).
 - b) a loss of cells in the blob region of V1.
 - c) a loss of binocularly driven cells in layer 4 of V1.
 - d) a loss of binocularly driven cells in layers above and below layer 4 of V1.
 - e) no permanent changes in visual ability.

2. Your patient has developed a sudden loss in his ability to read. The right side of any word that he looks at is not visible with either eye but he can see things in his peripheral vision. His problem is
 - a) macular degeneration.
 - b) compression of the optic chiasm.
 - c) a stroke affecting the posterior end of the calcarine sulcus on the right side.
 - d) a stroke affecting the anterior end of the calcarine sulcus on the right side.
 - e) a stroke affecting the posterior end of the calcarine sulcus on the left side.

Answers

1. d)
2. e)

See also <http://www.tutis.ca/NeuroMD/L2V123/V123Prob.swf>