

## Sensation and Perception

Everything you see or hear or experience in any way at all is specific to you. You create a universe by perceiving it, so everything in the universe you perceive is specific to you.

Douglas Adams, *Mostly Harmless*, 1993

Jean-Baptiste-Siméon Chardin, 1758

The painting illustrated in this slide – Chardin’s *Jar of Apricots* – is in the Art Gallery of Ontario. Chardin was a master of still life. His painting has much to say about sensation. It brilliantly represents the visual scene: the glints of light in the wine, the reflections of the window in the jar of preserved apricots, the highlights on the lemon, the steam rising from the cup, the shadow of the saucer, the confectionary box, the wrapped cakes. Most striking is the *trompe d’oeil* of the knife, which invites the viewer’s grasp. We anticipate the tastes to come.

Perception is an interaction between you and the world. The world gives us information which we interpret according to our past experience. As Douglas Adams remarks, perception is thus personal – the world we perceive is a world seen from our own viewpoint. No one else sees it exactly as we do.

### Brain and Mind: Course Outline

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| <p><b>1. Introduction.</b> Brain anatomy. Stroke. Neurons. Excitation. Action potentials. Synaptic transmission.. Body sensations. Braille.</p> <p><b>2. Moving to the Music.</b> Muscles. Stretch reflexes. Basal ganglia. Cerebellum. Parkinson’s Disease. Balance. Hearing. Speech and music.</p> <p><b>3. Sensation and Perception.</b> Taste and smell. Hunger and satiety. Vision. Visual fields. Motion. Recognizing faces and objects. Illusions.</p> <p><b>4. Consciousness.</b> Sleep, meditation, coma, epilepsy. Locked-in syndrome. Attention. Consciousness. Theory of mind. Split-brain studies – interpreter.</p> | <p><b>5. Learning and Memory.</b> Synaptic changes. Motor skills. Priming. Episodic vs semantic memory. Amnesia. Alzheimer’s Disease.</p> <p><b>6. Language and Emotion.</b> Language. Humans vs chimps. Aphasia. Dyslexia. Basic emotions. Autonomic Nervous System. Love and Hate. Music.</p> <p><b>7. Thought and Will.</b> Executive functions. Psychopathy. Brain networks (attention and default). Determinism. Free will.</p> <p><b>8. Madness and Wisdom.</b> Psychiatric diagnosis. Anxiety. Schizophrenia. Depression. Addiction. Maturation of brain. Mental speed. Ageing. Wisdom.</p> |
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**Sense of Taste**

There are five basic taste sensations: sweet, sour, salt, bitter, and umami.



Kikunae Ikeda  
(1864-1936)

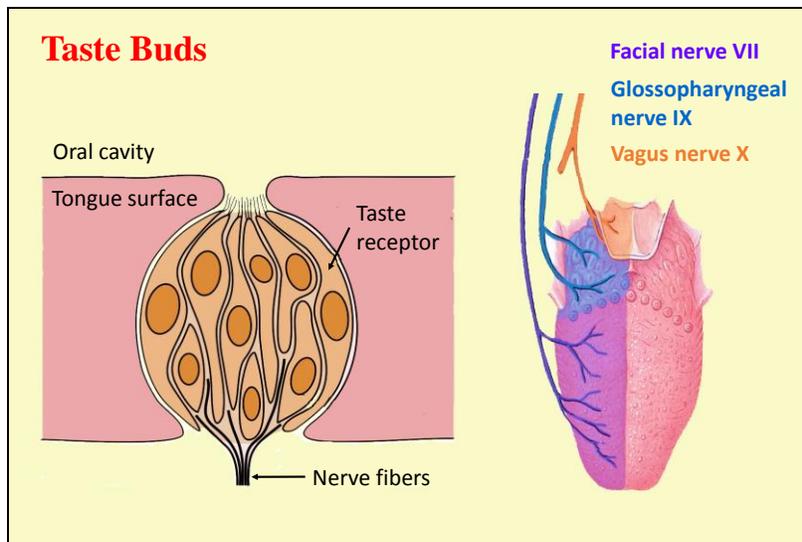


The surface of the tongue is covered with multiple papillae. Each of these contain many taste buds, each with receptor cells that respond to the different tastes. There is no special location for the different tastes.

Most of us were taught that there are four basic tastes. In 1908 Kikunae Ikeda proposed a fifth taste that was found in meat broths, soy sauce, and tomatoes – *umami* or “delicious.” This sensation is triggered by glutamate. Monosodium glutamate has become a common additive for foods.

The different tastes are perceived in small papillae (“nipples”) on the tongue. These are the tiny dots (a fraction of a mm) that you can see on the tongue. Those at the back are larger. The papillae contain taste buds which can process the different tastes that we experience.

It used to be thought that the different tastes were located in different parts of the tongue (sweet at the tip and bitter at the back) but more recent research has shown that there is actually no clear specialization of taste based on location.



The taste bud contains multiple receptor cells that react to the chemicals that diffuse from the surface of the tongue. Hairs on these cells are particularly sensitive to specific chemicals. Sour is

triggered by the hydrogen ion of acids, and salt by metallic cations such as sodium. Bitter and sweet are related to more complex molecular characteristics. Umami is triggered by glutamate. Three different cranial nerves carry the information from the taste buds.

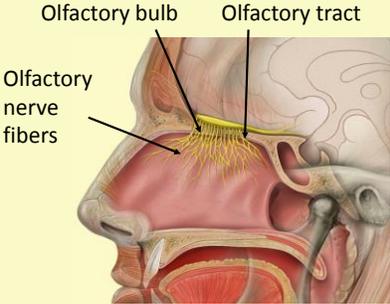
Our perception of “taste” also includes information about the food we are eating that is not mediated by taste buds. Spiciness (“hot”) and mintiness (“cool”) are detected in free nerve endings in the tongue and cheek. These are considered somatosensory sensations rather than visceral sensation and are carried to the brainstem by the trigeminal nerve (V). Astringency (tannins) and creaminess (fats) are other somatosensory sensations. The texture of food is not really a taste sensation, but it also contributes to our perception.

The most important additional information comes from our sense of smell. This is what makes an apple “taste” like an apple and a potato like a potato.

### Sense of Smell

Human beings can distinguish thousands of different odors. These may be classified into ten basic types:

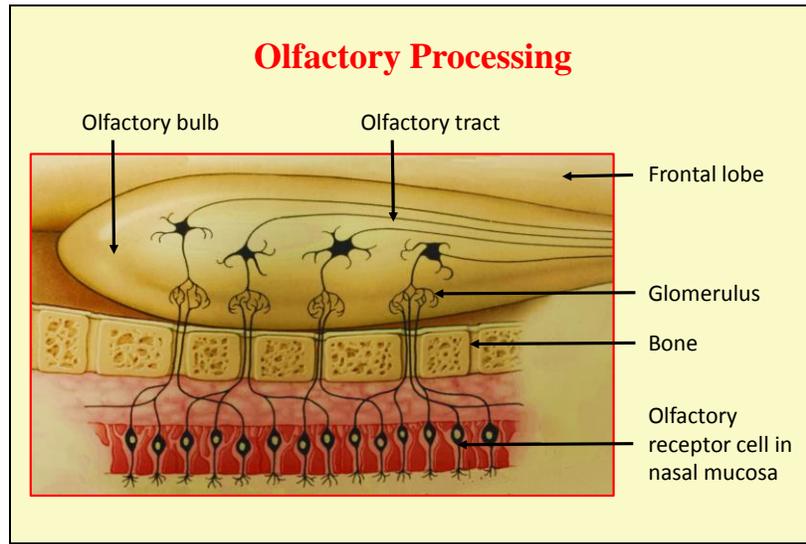
1. fragrant/floral
2. woody/earthy
3. fruity/sweet
4. rancid/putrid
5. chemical/etherish
6. mint/cool
7. vanilla/almond
8. nutty/buttery
9. garlic/onion
10. citrus/lemon



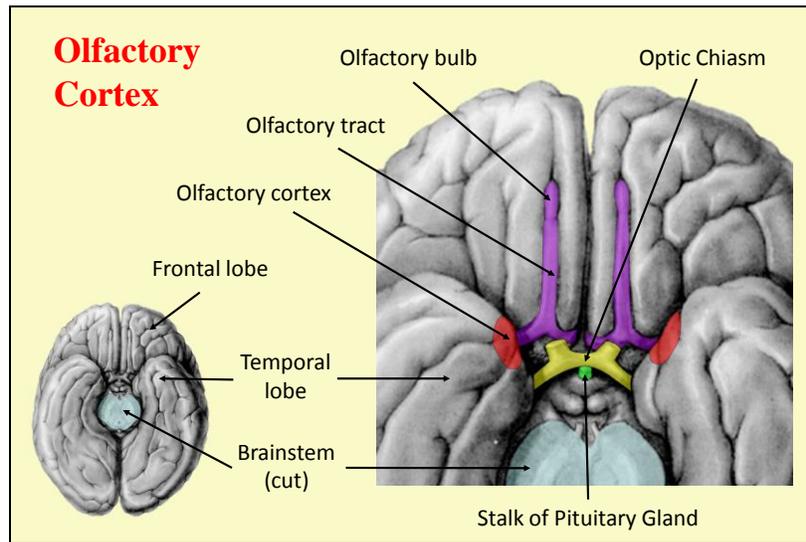
Olfactory nerve fibers have receptors that are activated by specific types of odors. This may be based on the structure of the odorant molecule (like a key into a lock) or on the vibration of the odorant molecules (like tuning a radio).

We can sense many thousand odors. We can distinguish (one odor from another) a much smaller number, and we can consistently identify an even smaller number. Many people have tried to categorize the basic sensations – the slide shows one such attempt. However, there is no consensus. One problem is how we perceive different mixtures of the hypothesized basic odors.

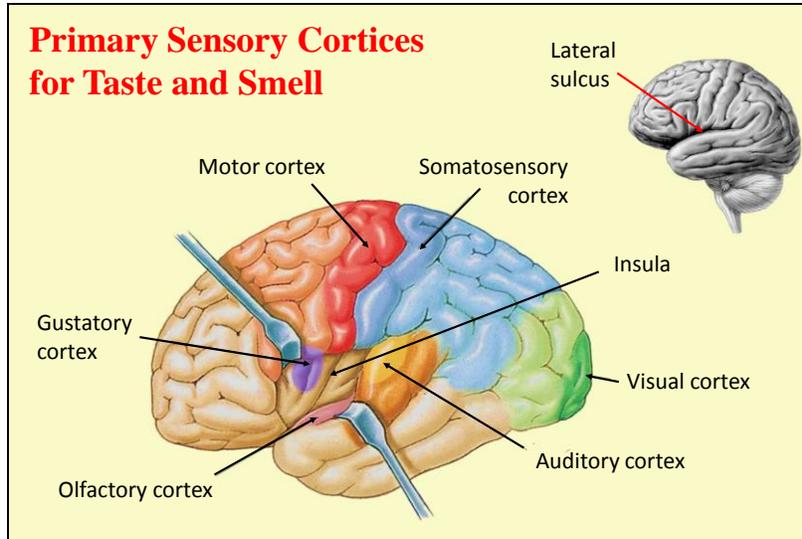
Most scientists think that odors activate the olfactory cells in the nasal mucosa by fitting into specially shaped receptors – like the transmitter molecules at a synapse. Another theory is that olfaction is based on the vibratory frequency of the molecules. This is espoused by Luca Turin, a scientist who has written a *Guide to Perfumes*. The difference between the two theories should be shown using molecules with deuterium instead of hydrogen. The results are controversial.



Olfactory receptors have endings on the surface of the nasal mucosa. They send their fibers through perforations in the bone at the top of the nasal cavity. These fibers form the olfactory nerve although they are not bundled together like other nerves. The fibers synapse with neurons in the olfactory bulb. These then project through the olfactory tract to regions of the insula and temporal lobe.



The slide shows the base of the brain. The olfactory tract is located below the frontal lobes. The olfactory cortex is located on the medial surface of the anterior temporal lobe. This is just anterior to the hippocampus which is concerned with memory. Smell is thus very closely associated with memory. The cortex is also rapidly in touch with the amygdala (in the temporal lobe) and the hypothalamus (above the optic chiasm) – both of which are involved in emotions.



This illustration shows the primary sensory cortices. We have already considered the somatosensory cortex (blue) on the postcentral gyrus. Retractors have opened up the lateral surface to show the auditory cortex (yellow) on the top of the temporal lobe, the olfactory cortex (pink) on the antero-medial aspect of the temporal lobe and the gustatory cortex (indigo) on the insula. The visual cortex (green) is at the occiput. The differently shaded regions are the secondary sensory cortices.

**Olfactory Control of Behavior**

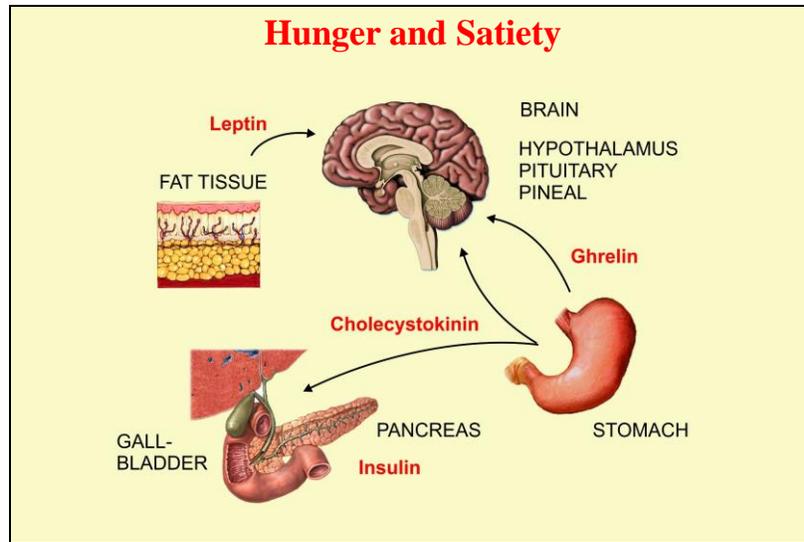
Our sense of smell tells us whether food is good, whether someone is attractive, and whether a place is enjoyable.

Most of its effects are subconscious.

The complex block contains four images: a spice rack with various colored powders, a man in a dark shirt smelling a flower, a man in a white lab coat smelling a woman's back, and a close-up of a large, vibrant rose.

Smell governs much of our behavior but it often does so without our being conscious of it. Food is made more attractive by the addition of spices. Axillary sweat can put people off – this has led to a huge deodorant industry. Some chemicals in our sweat can be attractive to the opposite sex. Several companies market male colognes with androstenone. Some studies have found that this is attractive to ovulating women, but others have disputed this. This has not stopped the ads which show beautiful young women chasing after an androstenone-scented male. Flowers and

musk form the main ingredients of perfumes. Chanel No 5 contains the scents of jasmine, rose and musk.

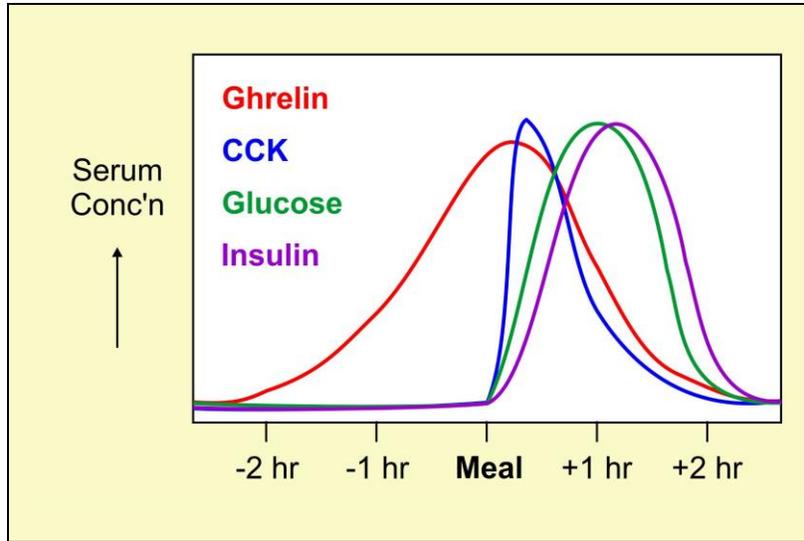


The chemical senses are very important in controlling feeding behavior. The aroma of fine food triggers our desire to eat. These effects are superimposed upon a complicated set of hormonal interactions.

The main “hunger hormone” that triggers our desire to eat is ghrelin – it is secreted by an empty stomach. It acts on the hypothalamus and other regions of the brain to initiate feeding activity. It also releases growth hormone from the pituitary gland – “ghre” comes from **g**rowth **h**ormone **r**eleasing

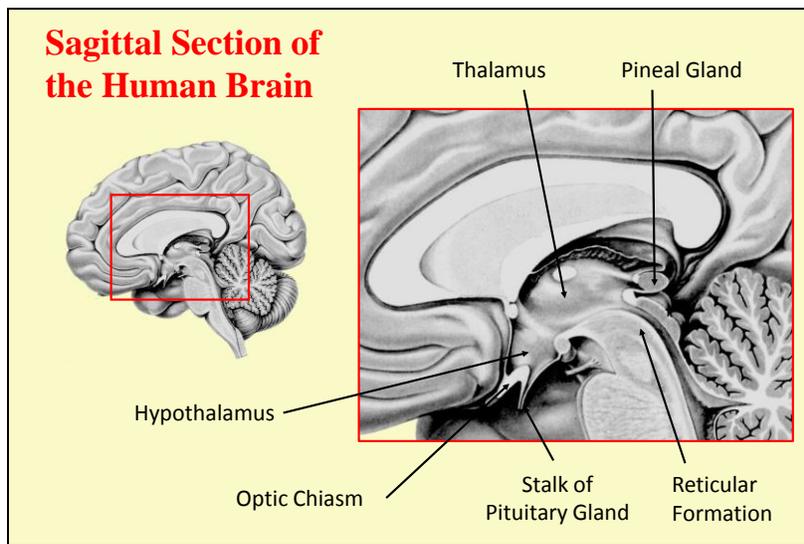
Once food is ingested, cholecystikinin (CCK) activates the bile duct to secrete bile salts. These help in the digestion of food in the small intestine. As foods are digested the blood sugar rises and insulin is secreted by special cells in the pancreas. Among its many actions insulin helps in the deposition of lipids in fat tissue.

Fat tissue secretes leptin – the “satiety hormone” (*lepto* means thin) – which decreases our overall desire to eat. However, the leptin cycle is much slower than our eating cycle. One possible reason for obesity is a resistance to leptin. Mice with abnormal leptin genes became hugely obese.



This shows the time course of hormones in relation to a meal. Ghrelin anticipates the meal and is inhibited once food is ingested. Cholecystokinin is secreted as soon as food is in the stomach. Once the food goes on to the small intestine sugar is absorbed. This triggers the release of insulin which causes the sugar to be absorbed into cells and used for energy metabolism or fat deposition.

Leptin follows a circadian rhythm. It depends on the amount of fat deposited.



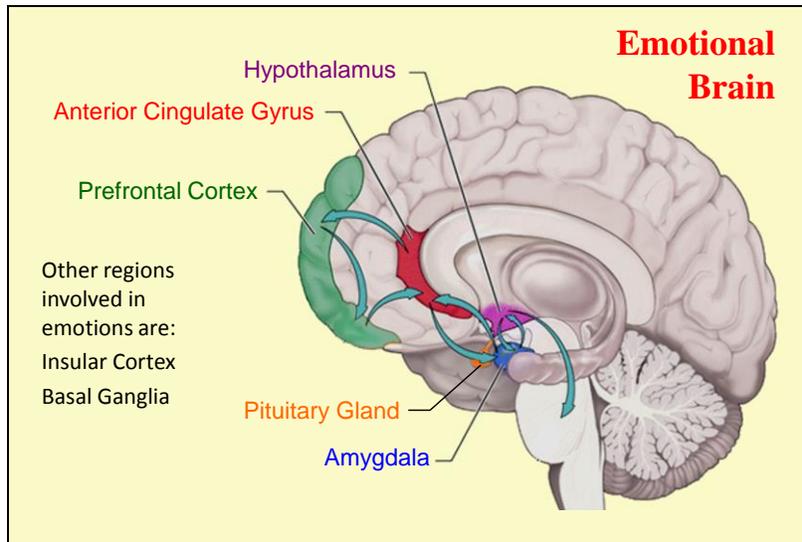
This anatomical illustration shows the parts of the brain that are important to maintaining basic bodily functions, of which feeding is one.

The pituitary gland supervises the other glands in the body. In this picture we just see the stalk of the pituitary. This is behind the optic chiasm.

The hypothalamus is right above the chiasm. The hypothalamus controls the “autonomic” nervous system. This system maintains the internal organs of the body and is largely

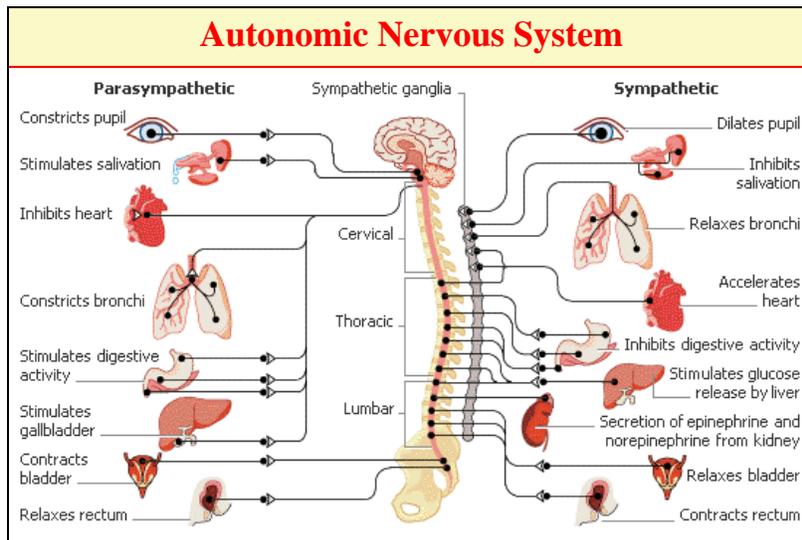
subconscious. It governs such things as the heart rate and the activity of the gut. “Autonomic” means that it runs by its own rules.

The pineal gland secretes melatonin which supports sleep and also interacts with hypothalamus.



Emotion exerts a major control over feeding. We shall see this slide again in later sessions concerned with emotion.

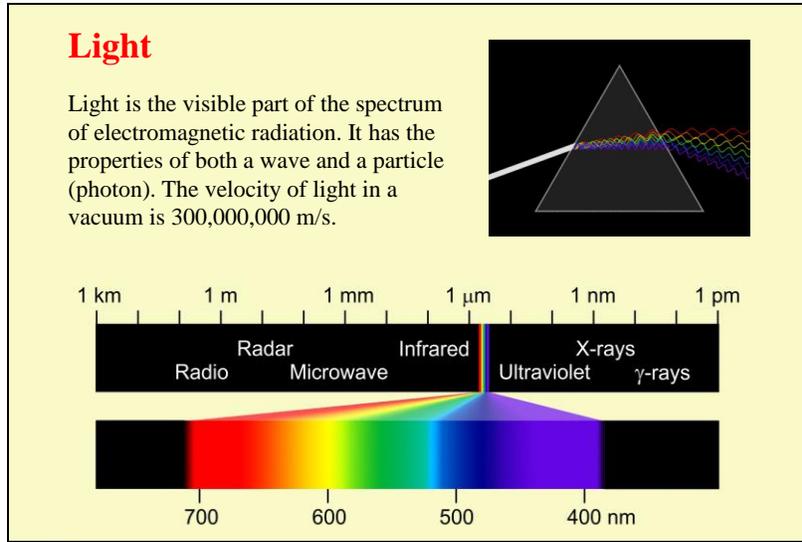
Many of the regions of the brain that are involved in emotion can be seen on the medial view. The prefrontal cortex mediates the conscious aspects of emotions. The hypothalamus and amygdala exert subconscious influences.



The autonomic nervous system controls our internal organs. Little of their activity reaches consciousness. Our insides follow their own rules.

Emotions change these activities greatly. Our heart beats faster, our mouth goes dry and our pupils dilate when we are emotionally aroused.

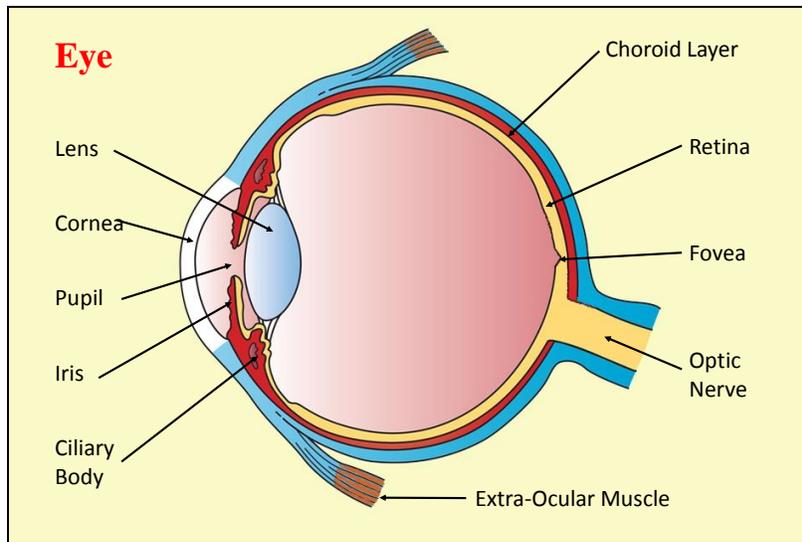
The autonomic system is affected by the emotions we are perceiving via the medial frontal lobes and the hypothalamus.



Now we shall move on to vision. The light that we can see is only a tiny part of the electromagnetic spectrum. Newton’s experiments in 1672 first showed how white light is composed of different colors.

What we see we normally perceive as colors. This is because we have three different types of light receptors in our retinas, each sensitive to a different region of the visible spectrum.

Most mammals other than primates have only two receptors – they are red-green color-blind. Some animals (birds, insects) perceive ultraviolet radiation.



This is a cross section of the human eye.

Light passes through the cornea. The pupil adjusts the amount of light entering the eye.

The lens acts to focus the light on the retina. Actually most of the focusing is done by the cornea, and the lens just increases this for near vision.

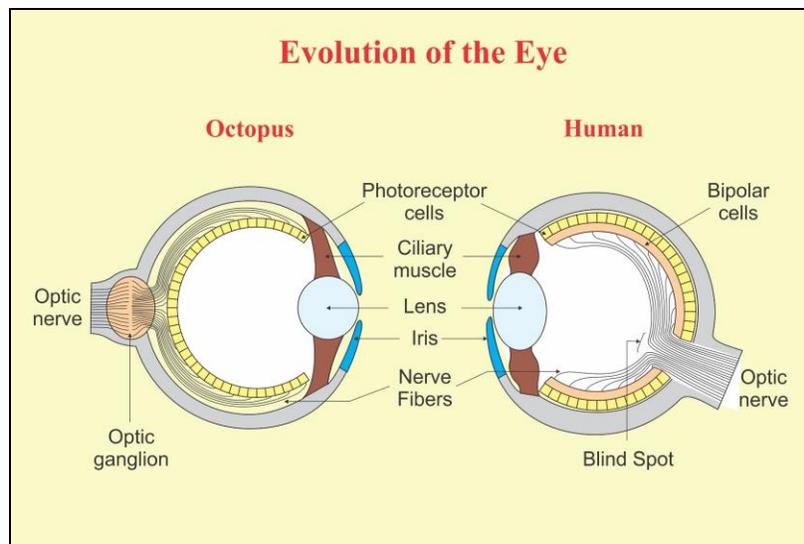
The extra-ocular muscles rotate the eye. The intra-ocular muscles are located in the ciliary muscle which adjusts the lens and in the iris which adjusts the pupil.

The light activates the receptor cells in the retina. The center of the visual field is at the fovea (a small depression).

The nerve fibers coming from the retina exit the eye through the optic disc to form the optic nerve.

At the optic disc there are no retinal cells – this is the “blind spot” about 12–15° laterally to the center of the visual field.

The blue layer is the protective “sclera” (hard). This is continuous with the transparent cornea.



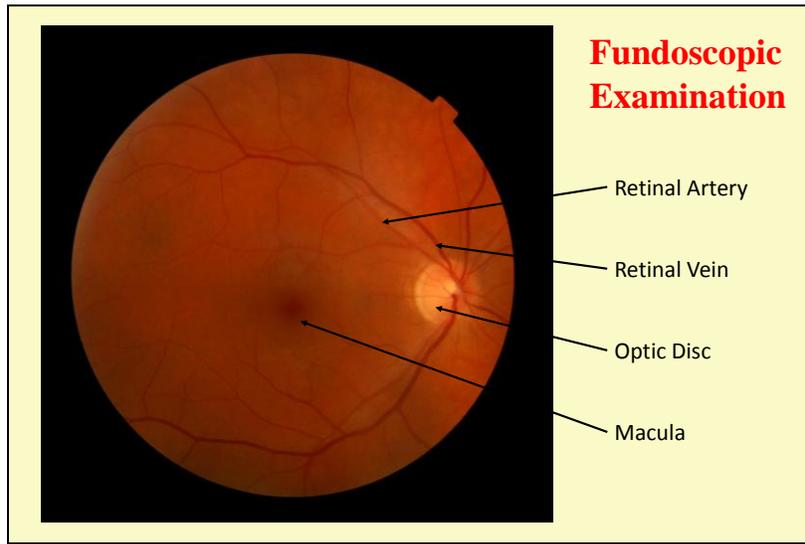
The octopus eye is remarkably similar to the human eye even though the two species are really far apart on the evolutionary tree.

They both act as pinhole cameras to focus images on the photoreceptors. The octopus eye has a pupil, lens and muscle to operate the lens just like the human eye.

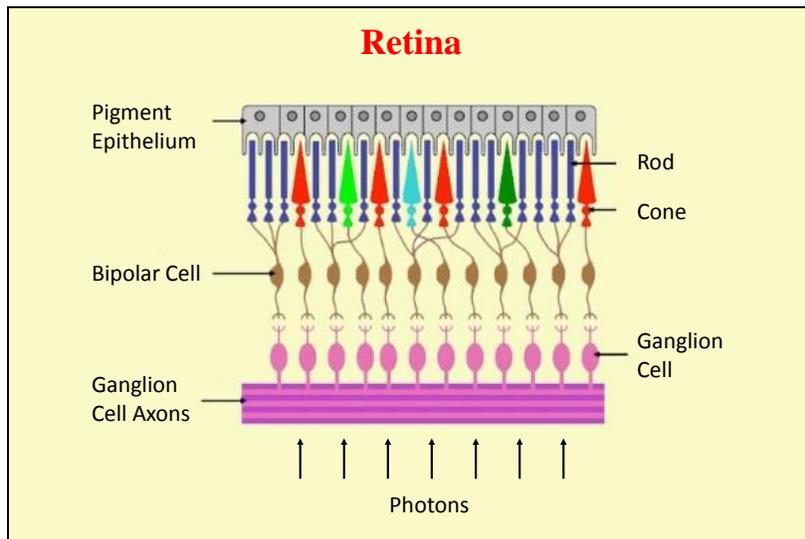
However the light falls directly on the photoreceptor cells in the octopus eye. It does not have to go through the nerve cells as it does in the human eye.

The embryological development of the two eyes is different. The octopus retina develops from an invagination of the skin whereas the human retina develops from an outpouching of the brain.

There are two fascinating conclusions. First, evolution can settle on a good design even in completely different species. Second, we are not sure whether there is any benefit to the backward structure of the human eye (or whether it is a design-flaw).



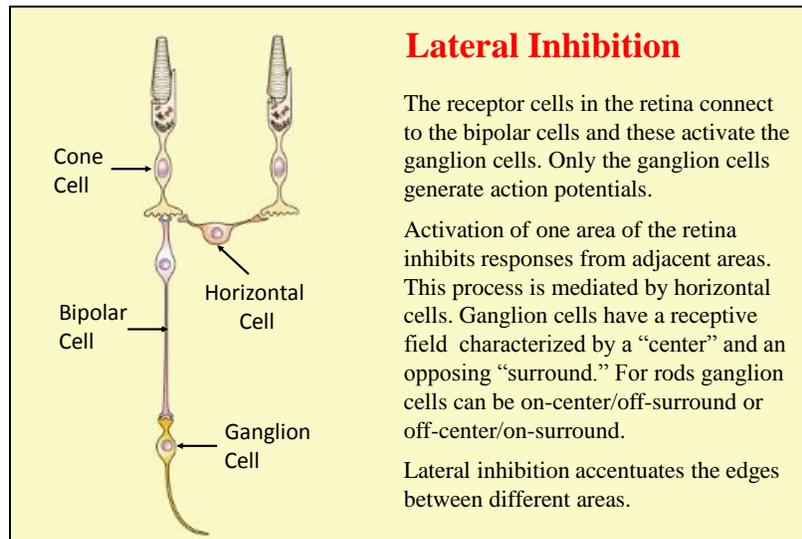
This is what is seen when an ophthalmoscope is used to look at the bottom (fundus) of the eye. Sometimes your optometrist will take a picture. Arteries and veins are in front of the retina. At the region of the fovea and the surrounding macula (stain) there are no large arteries or veins. The macula region is redder than the more peripheral retina. This is due to the many capillaries in that region.



The receptor cells of the retina are the rods and cones. These are activated by light – photons interact with membrane proteins and change the membrane potential in the receptor cells.

The receptor cells then activate bipolar cells. These synapse with the ganglion cells which send axons out of the retina through the optic disc, optic nerve and optic tract to the geniculate body in the back of the thalamus.

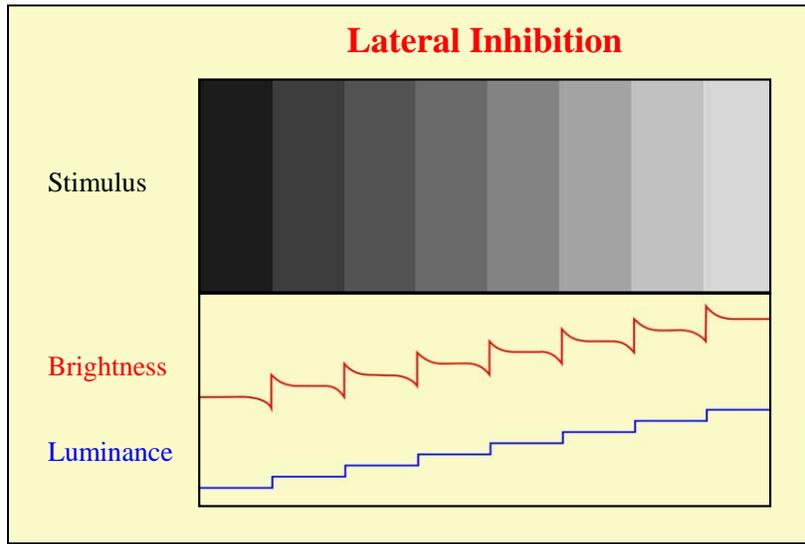
What is counter-intuitive about this arrangement is that the light has to go through the ganglion cells and bipolar cells before it reaches the rods and cones. Omitted from the diagram are the retinal arteries and veins which rest on inner surface of the retina – another impediment to the passage of photons.



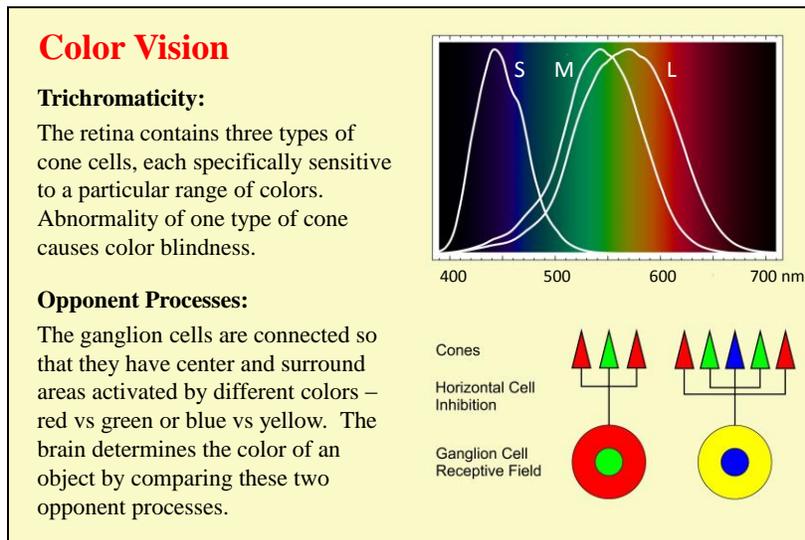
One of the main principles of vision (and indeed of all sensory systems) is lateral inhibition. Activation of one sensory area inhibits the activity of adjacent areas. This inhibition is mainly mediated by the horizontal cells of the retina.

The visual field of a ganglion cell may have a center where it is excited (on-center) plus a surrounding region where it is inhibited (off-surround). Or an off-center and on-surround.

Lateral inhibition helps us to recognize edges and outlines.



This shows how lateral inhibition accentuates the edges between regions of different luminance.

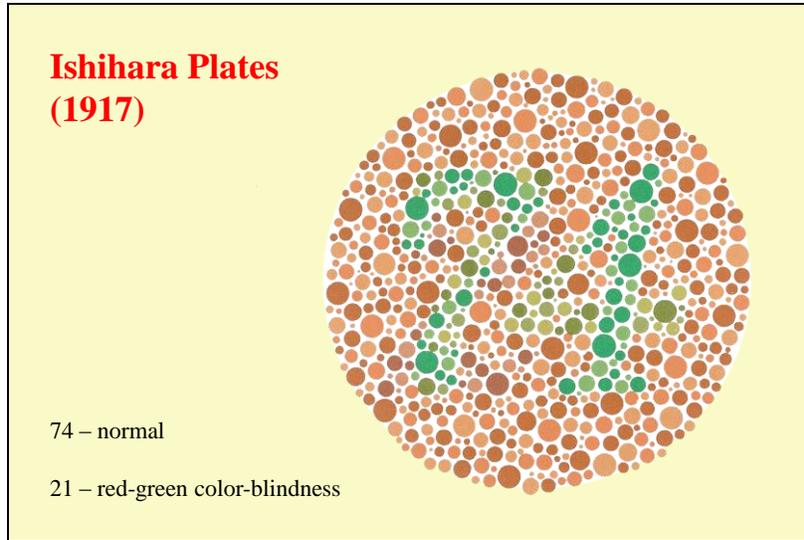


The retina contains three types of cones. (S, M, L mean short medium and long in terms of wavelength).

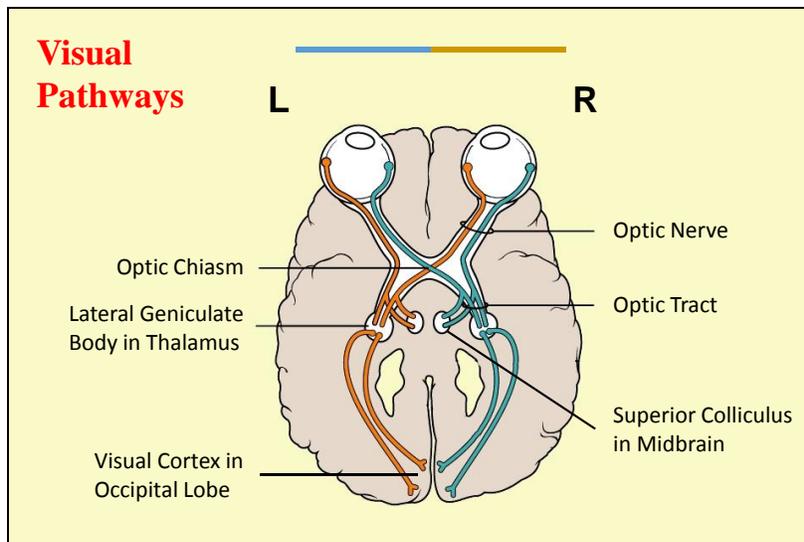
The cones are most concentrated in the center of the visual field. There is little color the periphery of our vision.

The most common type of color-blindness is an abnormality of the M type of photoreceptor. The subject has difficulty telling red from green. This disorder is determined by an abnormality on the X-chromosome. It is therefore sex-linked recessive. It occur is about 6% of males (and 0.36 % of females –  $0.06 * 0.06$  ).

The retina works by trichromaticity. The visual neurons work by opponency. Opponent processes compare the excitation between different receptors (or groups of receptors). The two types of opponent processes are red vs green and blue vs yellow.



This is one of the plates in the test for color blindness put together by Shinobu Ishihara at the University of Tokyo in 1917. Some of the plates cannot be read by the color blind. Others such as this one are read in two different ways depending on whether the viewer has normal vision or color-blindness. Depending upon the projector, this may or may not work – the plates are very carefully controlled for their color, but projections vary with the color of the light.

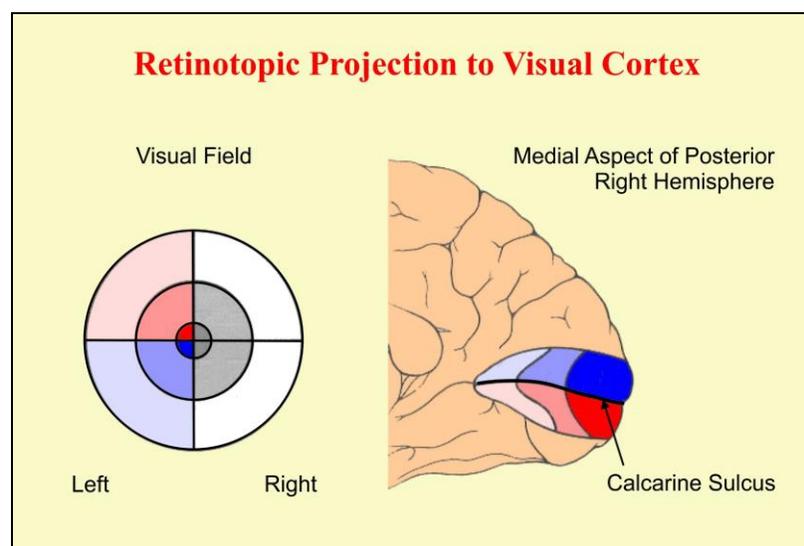


Each eye receives input from both the left and right side of the visual field. Because of the lens, the image focused on the retina is reversed – up is down and left is right.

In this diagram the right side of the visual field sends photons to the left side of the retina (yellow). The yellow fibers from the right eye cross over in the optic chiasm to join the uncrossed yellow fibers in the left eye and go through the left optic tract to the left lateral geniculate body (at the back of the thalamus) and thence to the visual cortex in the left occipital lobe. Thus the right visual field as seen by either the left or the right eye projects to the left visual cortex.

The opposite occurs for the photons arriving from the left side.

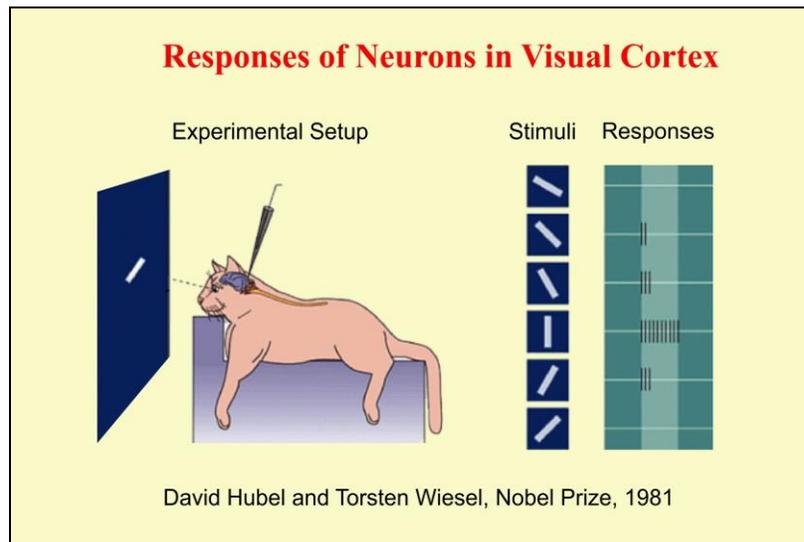
The superior colliculus in the midbrain is a region that helps control eye-movements.



The left visual field projects to the visual cortex on medial surface of the right occipital lobe around the calcarine sulcus.

The visual field is distributed over the visual cortex with the fovea at the occipital pole and the lateral limits of the visual field more anterior.

The foveal region of the visual field (where we have our most precise vision) takes up much more cortical surface area than the other regions of the visual field.



This shows the experimental set-up for examining the responses of neurons in the cat visual cortex.

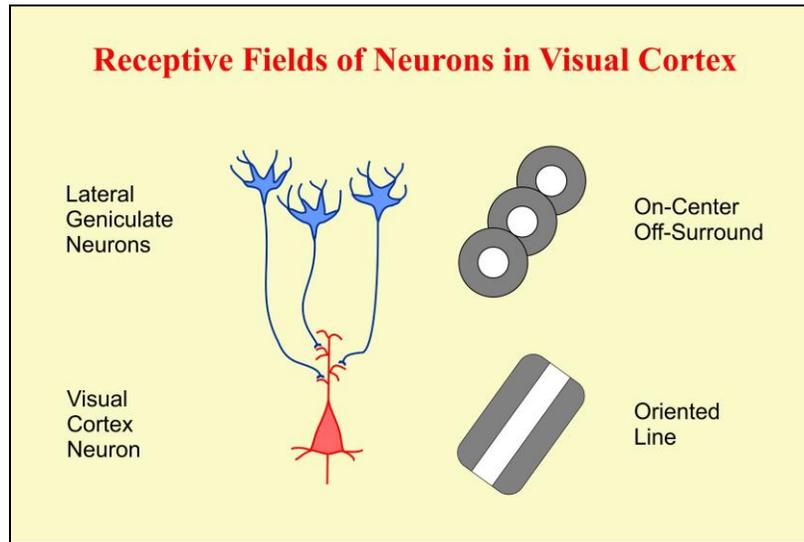
Most of the neurons in the primary visual cortex respond to oriented lines. As the bright line is moved across the receptive field of the neuron, the response varies with its orientation. These experiments were performed by the Canadian David Hubel and the Swede Torsten Wiesel, while they were working at Harvard University. They shared the Nobel Prize in 1981.

The video in the presentation shows Hubel and Wiesel mapping the receptive field of a neuron in the cat's visual cortex.

The neuronal response is amplified and played on a speaker.

The full video is at

<https://www.youtube.com/watch?v=8VdFf3egwfg>



The neurons in the lateral geniculate body have receptor field that are almost identical to those in the ganglion cells of the retina. They have on-centers and off-surrounds or vice versa. Multiple neurons in the geniculate connect with one neuron in the cortex. The connections are arranged to make the cortical neurons act as orientation-sensitive line- or edge-detectors.



### Migraine

Migraine is a severe, throbbing headache, lasting between 2 and 72 hours, usually involving only one side of the head, and often associated with light-sensitivity, nausea and vomiting. Migraine occurs in about 6% of men and 18% of women in any one year, and is most common between the ages of 20 and 50 years.

In about a third of the cases, the headache is preceded by an “aura” lasting about 20-30 minutes. The most common aura affects the visual system – a “scintillating scotoma.” A small region of visual loss slowly expands to involve half the visual field. At the edge of the visual loss is a border of flickering zig-zag shapes. The visual aura may begin with a focal release of potassium ions in the visual cortex. This excites the neurons, releasing more potassium until the neurons become inactive. A wave of excitation-depression then slowly spreads across the cortex.

Migraine is a common cause for headache.

We do not know its cause but the pain probably involves brainstem neurons connected to the trigeminal nerve. The headache also involves the dilation of blood vessels in the head. Sometimes the headache is preceded by an aura. The most common type is the scintillating scotoma (sparkling blindness).

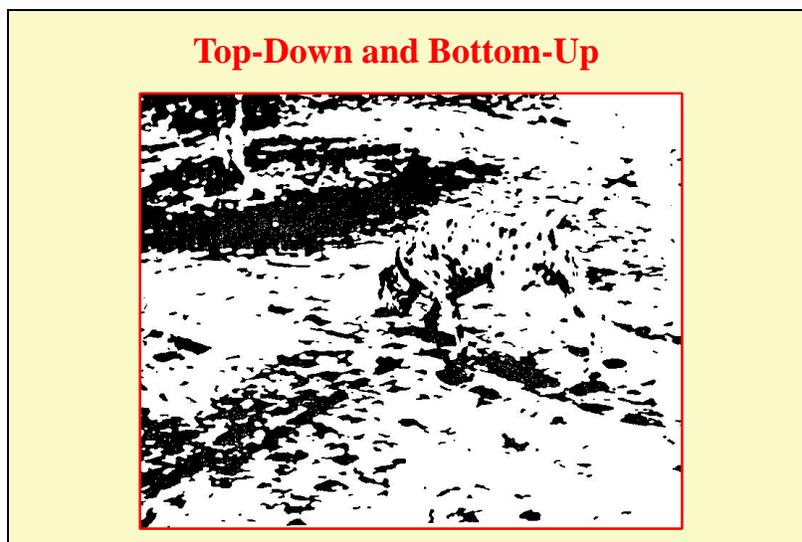
This is likely triggered by some vascular problem in the visual cortex and spreads from one region to another. One theory involves a spreading release of potassium ions that excite and then exhaust the neurons.

The patient often perceives zig-zag lines at the edge of the scotoma, probably as if multiple Hubel-Wiesel neurons were discharging.



This video from the Mayo Clinic is a simulation of the scintillating scotoma that one might see in a migraine aura. The simulation is about ten times faster than in real life.

<https://www.youtube.com/watch?v=qVFicF9lyk8>



Now we shall move on to visual processing that involves seeing more complicated objects than simple lines. Our brains are particularly adept at seeing objects in the world – often on the basis of minimal information. Visual perception combines information coming in from the eyes with

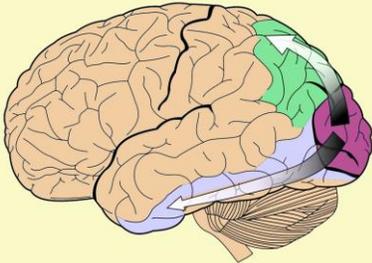
expectations and hypotheses about what it might mean. This picture initially looks like a bunch of black dots. However, if we try hard to see things in the picture we can make out a Dalmatian dog rooting about in the leaves. Once we finally see the dog (or if it is pointed out), it becomes obvious. Sometimes we note how things move – an object is something the parts of which move together.

### Dorsal and Ventral Streams

**Where?**  
Information from the **visual cortex** goes to the **parietal lobe** to be used for controlling movement in space such as reaching and grasping.




**What?**  
Information goes to the **temporal lobe** to be used to identify objects and people.



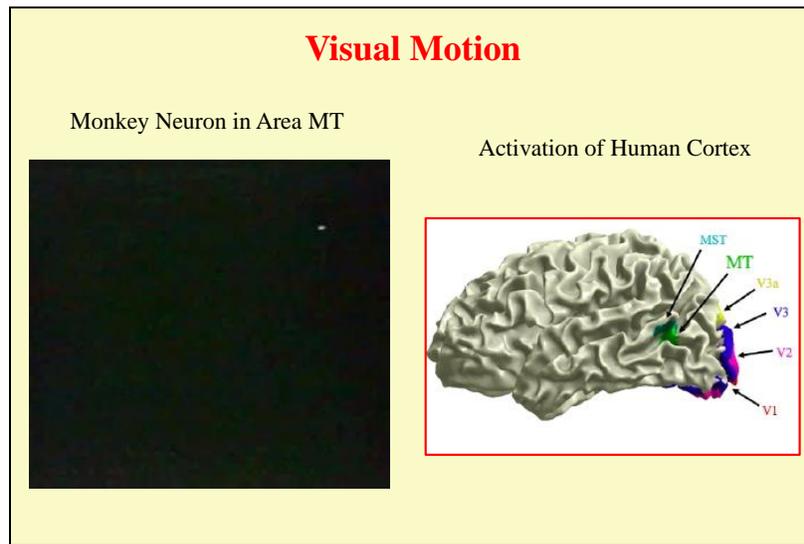
Melvyn Goodale, 2014

After the visual cortices in the occipital lobe (purple), visual information travels into two different perceptual systems.

The “where” system in the parietal lobe (green) is used for controlling movements in space. The pictures in the lower right of the slide show the regions of the brain that are active when a small object is being manipulated. These experiments were performed by Mel Goodale and his associates at the University of Western Ontario.

The “what” system is in the lower temporal lobe (pale blue).

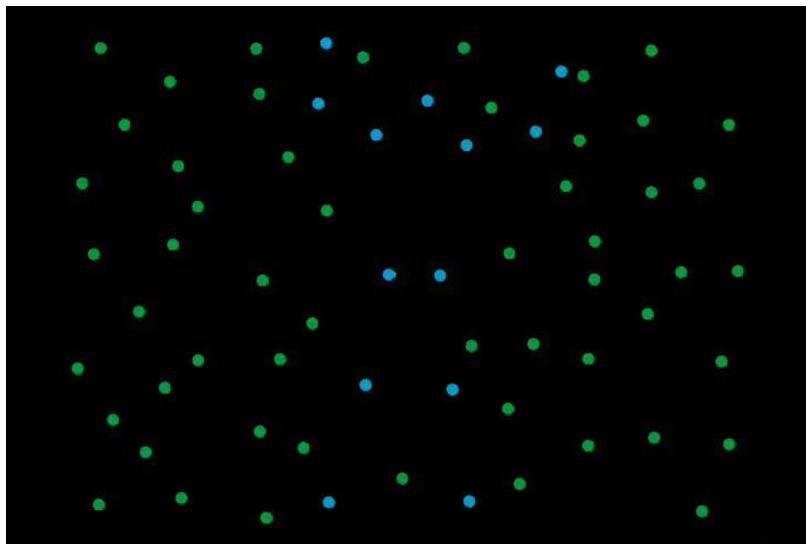
Motion perception is important to both what and where. Visual control requires knowledge of how things are moving. The perception of objects requires looking at how they move – an object is all the parts of the visual input that move together. Motion is processed between the two visual streams in an area called MT.



A special area of cortex called MT (middle temporal) or V5 is specifically sensitive to motion. This area connects to the parietal lobe – for control of movement – and to the temporal lobe – for object detection.

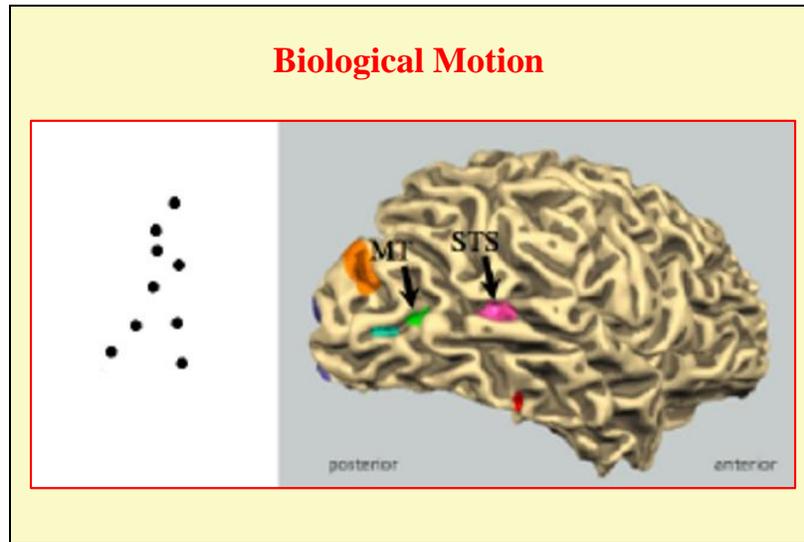
Video can be obtained in QuickTime format from

<http://www.cns.nyu.edu/~david/courses/perception/lecturenotes/motion/motion-slides/newsome-direction.mov>



This video illustrates the perception of biological motion. Our nervous system perceives human movements even in very simplified input – dots or lines. We are predisposed to see other human beings and we can recognize an individual from a distance from the way he or she walks.

The music is from the Miles Davies record *Kind of Blue*. The track is *Blue in Green* with John Coltrane on saxophone and Bill Evans' on piano.



Biological motion is specifically detected in the STS (superior temporal sulcus) region of the brain.

**Visual Agnosia**

**Oliver Sacks**  
1933-2015

*The Man Who Mistook His Wife for a Hat* (1985)

‘What is this?’ I asked, holding up a glove.  
‘May I examine it?’ he asked, and, taking it from me, he proceeded to examine it as he had examined the geometrical shapes.  
‘A continuous surface,’ he announced at last, ‘infolded on itself. It appears to have’— he hesitated— ‘five outpouchings, if this is the word.’  
‘Yes,’ I said cautiously. ‘You have given me a description. Now tell me what it is.’  
‘A container of some sort?’  
‘Yes,’ I said, ‘and what would it contain?’  
‘It would contain its contents!’ said Dr P., with a laugh. ‘There are many possibilities. It could be a change purse, for example, for coins of five sizes. It could ...’

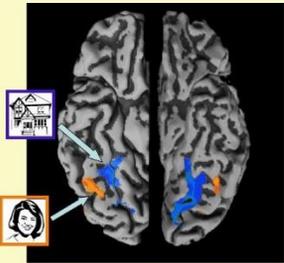
Visual perception can be disordered by lesions to the inferior temporal regions. These can lead to agnosia.

The patient with agnosia can see an object but is unable to recognize what it is. Such a patient was reported by Oliver Sacks in his famous case study of *The Man who Mistook his Wife for a Hat*. Oliver Sacks died last year.

The brain that Dr. Sachs is holding is the same as the plastic brain that I showed you during the first session.

**Face Perception**

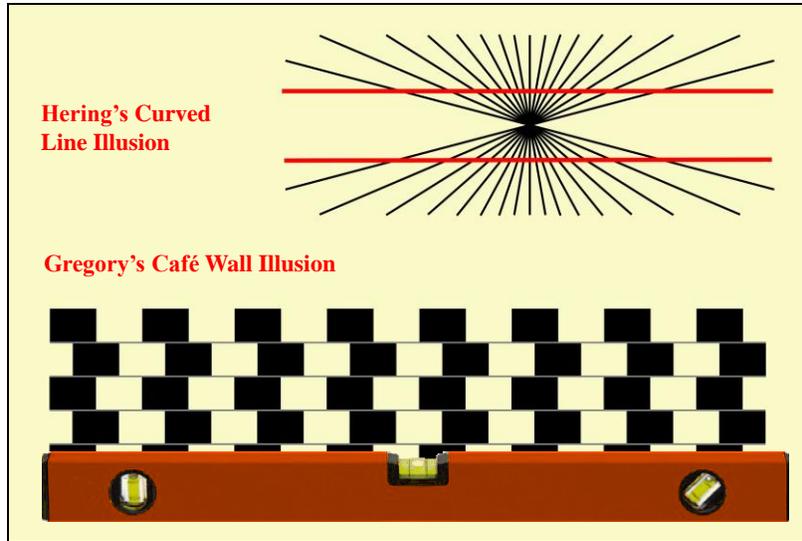
The fusiform gyrus on the inferior surface of the temporal and occipital lobes is specialized for the perception of faces. Bilateral damage to these regions causes “prosopagnosia” – the inability to recognize faces.



Giuseppe Arcimboldo, 1591

The lower surface of the temporal lobe is specialized for perceiving faces and objects. Bilateral lesions to this area causes a special type of agnosia – prosopagnosia, the inability to recognize faces.

In an intriguing study, Morris Moscovitch found out that patients with prosopagnosia were also unable to see the faces in the vegetable portraits of Giuseppe Arcimboldo. Oliver Sacks actually suffered from congenital prosopagnosia and wrote about it in the *New Yorker* in 2010.

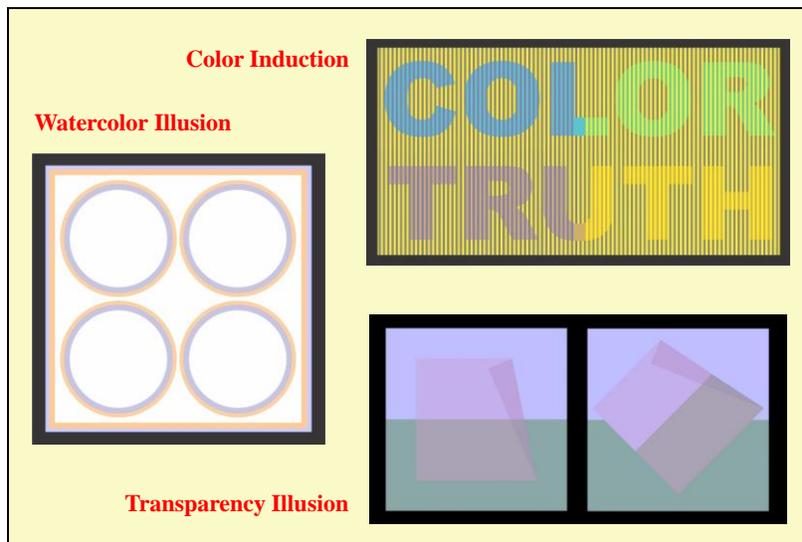


Visual illusions are common. They help us to understand how the visual system works.

We quickly learn that things may not always look the way they are, and we often double-check our perception using a different view.

Despite the illusion of the tilting tiles in Richard Gregory's café-wall, we can prove with a spirit level that they are actually all horizontal.

We can similarly prove that the red lines in the Hering Illusion are not curved.

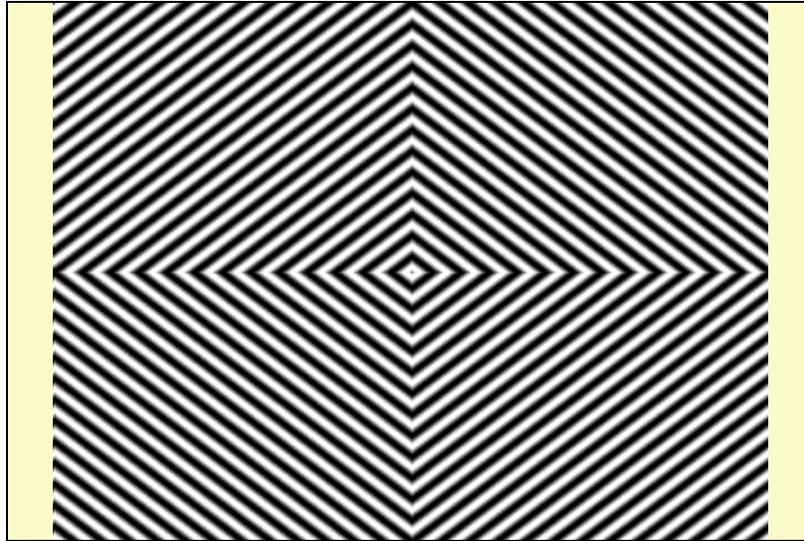


These are some illusions that derive from how we perceive color.

In the watercolor illusion, the spaces inside and the outside of the circles are both the same shade of white.

In the color induction example, the letters behind the grid are the same color (the turquoise and orange shown in the middle) on the left and on the right.

In the transparency illusion the picture on the left is interpreted as a transparent film. Rotation shows that it is not transparent.



This is an illusion based on perceived movement. It is like the waterfall illusion – staring at a waterfall for a while and then looking at the neighboring rocks or trees will suggest these stationary objects are rising (motion after-effect).

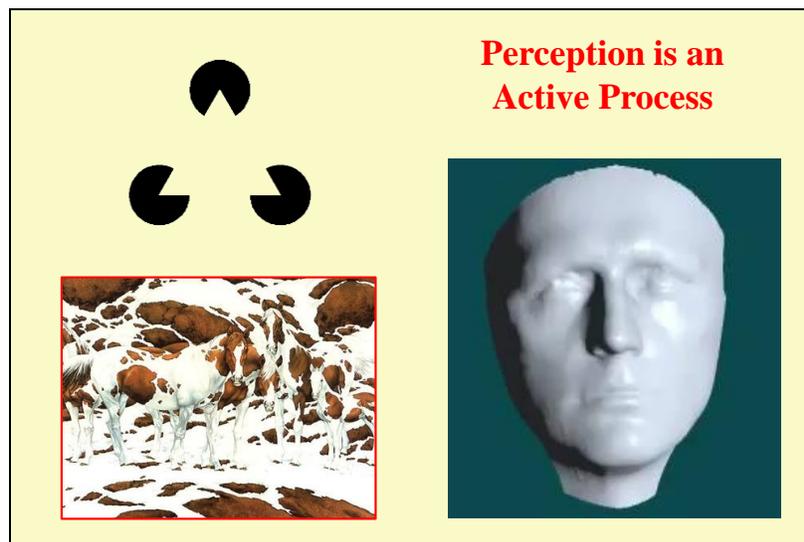
If you look at this stimulus for thirty seconds and then look at the back of your hand, it will appear as if things are growing under the skin.

This particular stimulus comes from Wikipedia

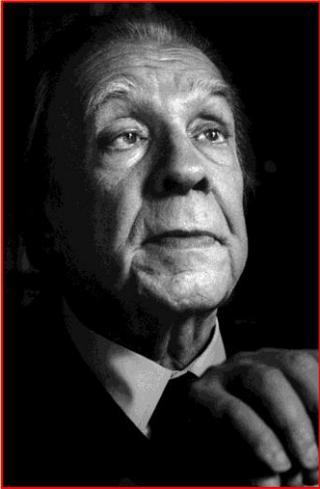
[https://en.wikipedia.org/wiki/Motion\\_aftereffect](https://en.wikipedia.org/wiki/Motion_aftereffect)

This amazing webpage has many different visual illusions

<http://www.michaelbach.de/ot/>



Perception is therefore a creative process. We see what makes sense. A white triangle over three black disks makes more sense than three discs with sections removed. A normal face is much more common than the inside of a mask. We can see the pinto horses in the snow if we know what we are looking for.



**Jorge Luis Borges (1899-1986)**

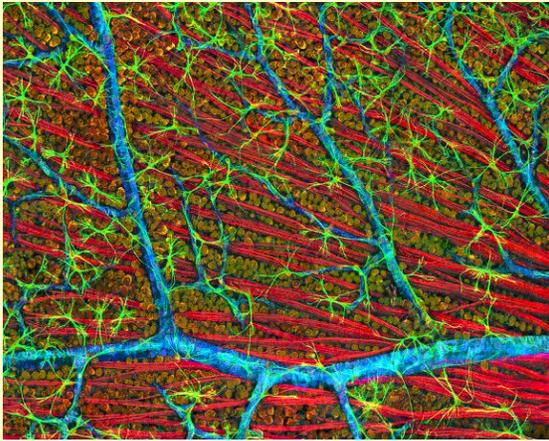
I saw the teeming sea; I saw daybreak and nightfall; I saw the multitudes of America; I saw a silvery cobweb in the center of a black pyramid; I saw a splintered labyrinth (it was London); I saw, close up, unending eyes watching themselves in me as in a mirror; I saw all the mirrors on earth and none of them reflected me; I saw in a backyard of Soler Street the same tiles that thirty years before I'd seen in the entrance of a house in Fray Bentos; I saw bunches of grapes, snow, tobacco, lodes of metal, steam; I saw convex equatorial deserts and each one of their grains of sand ... (*El Aleph*, 1946)

Because of top-down processes, perception can occur without sensation – the imagination. This is the Argentinian writer Borges. Toward the end of his life he became blind. Yet he could always see things in his imagination. The passage is from one of his famous stories.

**Sensation  
&  
Perception**

A lover's eyes will  
gaze an eagle blind

*Love's Labour's Lost*  
IV:3 Shakespeare



Retina, Thomas Deerinck, 2006

This specially colored microscopic view of the surface of the mouse retina shows the blood vessels in blue, the ganglion cells in brown, their axons in red and the glial cells in green. You cannot see the rods and cones – the light has to cross all of these cells before activating the photoreceptors.