

The illustration shows the hairs in the cochlea.

The quotation is from Aldous Huxley. He was an older half-brother of Andrew Huxley, who much later studied action potentials in squid giant axons.

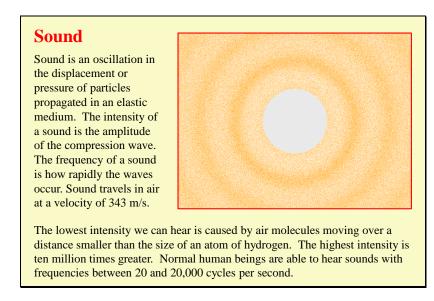
The music is Bach's Orchestral Suite #2 in B minor.

At the end of last week's session we looked at the vestibular sensory system. The week before we considered the somatosensory system.

This week we shall consider two of the special senses: hearing and seeing. And talk a little about perception – when we pay attention to our senses.

We shall not be able to cover the senses of taste and smell. Too many senses too little time.

Today will be divided in two; the first half for hearing, the second for seeing. In each section we shall learn a little bit about how the receptors work, how the brain processes information from those receptors, and what can go wrong when the receptors or the brain malfunction.



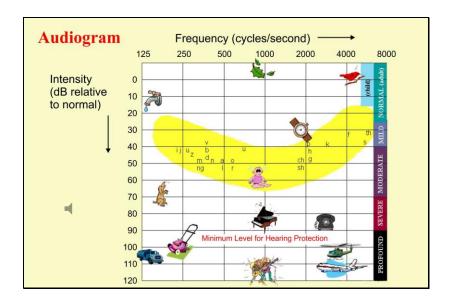
When sound is made, molecules are compressed – they then expand and compress other molecules further away from the source and the "sound' travels through the medium. Despite the movies there is no sound in space because there are no molecules to compress. Sound travels at 1200 km/hr in air. It travels more quickly in water and even more quickly in iron.

Sound has three main characteristics - frequency (pitch), intensity (loudness) and location.

The original illustration (which moves) comes from https://en.wikipedia.org/wiki/Sound#/media/File:Spherical pressure waves.gif

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As we get older we typically start to lose our ability to hear high frequencies. The animated illustration of sound frequencies can be obtained at https://www.youtube.com/watch?v=H-iCZEIJ8m0



Hearing is tested by plotting the threshold for hearing a tone of a particular frequency against the normal hearing thresholds – the audiogram. Intensity is typically considered in logarithmic terms (deciBels or dB) because of the huge range from threshold sounds to loud sounds.

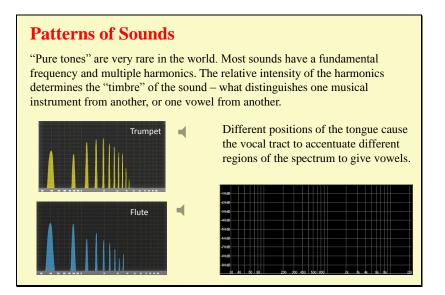
To measure the audiogram, tones are decreased in intensity until you cannot hear them any more. Threshold is the lowest level you at which you can hear.

Someone with normal hearing has thresholds near 0 dB on the audiogram.

Someone with a hearing loss would only hear the louder tones and would therefore have thresholds plotted lower down on the graph.

Normal conversational speech sounds occur in the yellow banana-shaped region of the audiogram – between 200 and 8000 cycles per second and from 20 to 60 dB above normal thresholds.

You should protect your ears against sounds over 90 dB above normal thresholds – especially jet planes and rock bands. Anything that causes a ringing in the ears (tinnitus). Even though there may be no change in hearing threshold, there is still loss of neurons. As time passes this will lead to threshold elevation.

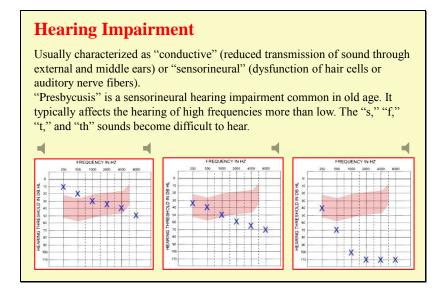


In order to discriminate one vowel from another the ear has to recognize the different frequencies in a sound. These diagrams plot the "spectra" of the different sounds. These show the energy level of the sound (y-axis) against the frequencies that are present in the sound (x-axis). Thus the trumpet sound has a fundamental frequency and a set of harmonics (multiples of that frequency)

For the trumpet the high harmonics are louder than the fundamental. The louder the higher harmonics the "brassier" the sound. The flute has higher harmonics but these are less intense than the fundamental – the flute sounds "pure"

We use the same techniques to identify the different vowels by which harmonics are accentuated. For the ah and oh sounds the harmonics are mainly at low and middle frequencies; for the ee sound there is one low region and one region of accentuated harmonics at high frequency. The video of the vowel spectra are shown on

https://www.youtube.com/watch?v=-Zf0YEh262o



The examples for mild and moderate hearing loss are what you might hear if you had a hearing loss. My own hearing loss is similar to that shown in the middle.

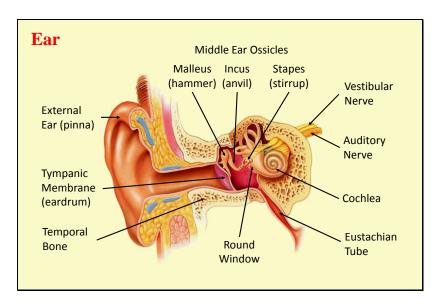
The severe to profound hearing loss shows what the words might sound after amplification. Only the low frequencies are clearly audible. The sounds of speech become wa wa wa

Samples of what a hearing loss might sound like are available at <a href="http://www.hearinglikeme.com/hearing-loss-simulator-understanding-mild-and-moderate-hearing-loss/">http://www.hearinglikeme.com/hearing-loss-simulator-understanding-mild-and-moderate-hearing-loss/</a>



A variety of hearing aids can be used to amplify sounds and thereby assist hearing. These can be in or behind the ear.

The aids can be adjusted to a patient's particular hearing configuration. They can also use special programs that distinguish speech sounds from background noise.



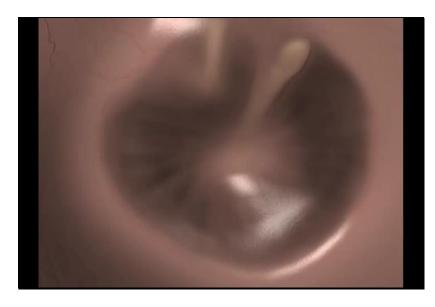
The ear is customarily divided into three parts: external, middle and internal.

The external ear consists of the pinna and the external ear canal. The pinna can help in the localization of sounds though this is less important in humans than in other mammals such as dogs and bats.

The middle ear begins at the ear drum. It contains three small bones - hammer, anvil and stirrup. The eardrum and these ossicles convert the large-amplitude low-force vibrations of the air molecules to small amplitude high-force vibrations at the oval window. Thus the sound signal is transferred from gas to fluid with little loss of energy.

The Eustachian tube connects the middle ear to the back of the throat. It equalizes the pressure across the tympanic membrane. It is normally opened by swallowing. This is what has to be opened when you descend in an airplane. Holding your nose, blowing and then swallowing helps.

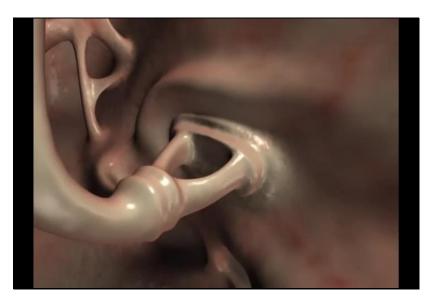
The inner ear contains both the vestibular system, which measures balance, and the cochlea, which measures hearing.



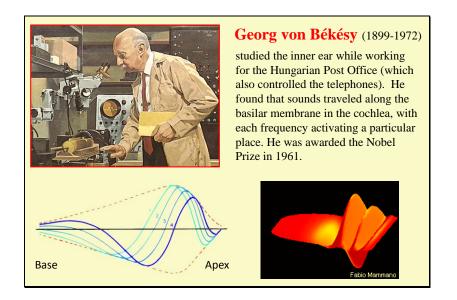
To understand the process of hearing, it is essential to see what happens in the ear as sound arrives.

First how the middle ear works to transfer the sound from the air to the fluids in the inner ear. This and the subsequent video come from

https://www.youtube.com/watch?v=PeTriGTENoc



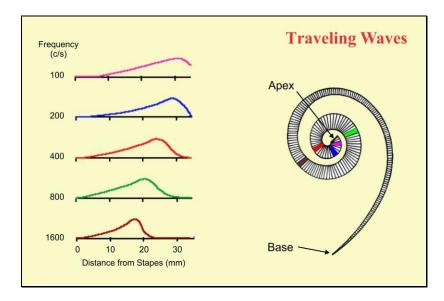
Now how the inner ear works – how the vibrations entering through the oval window activate the cochlea.



The vibrations of the oval window set up a traveling wave on the basilar membrane. This moves down the basilar membrane (upon which the auditory sensory organs rest) from the base of the cochlea (near the oval window) to the apex. The location on the basilar membrane that is most displaced depends on the frequency of the sound. Low frequencies cause their maximal displacement near the apex. High frequencies activate the base.

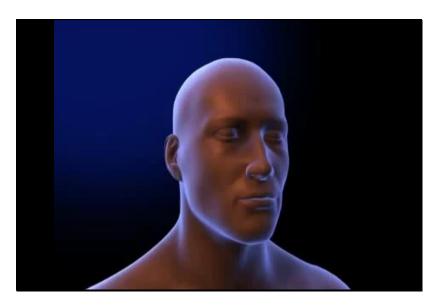
The animation by Franco Mammano exaggerates the relative width of the basilar membrane. The oval window is at the left above the membrane.

The round window is below. Changes in pressure from above to below the basilar membrane travel along the membrane toward the apex.



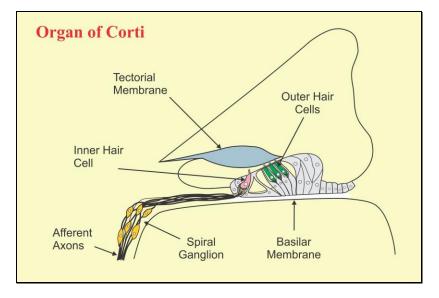
The human cochlea makes  $2\frac{1}{2}$  turns from the base where the oval window vibrates to the apex. The width of the basilar membrane increases and its stiffness decreases as we go from base to apex. This causes it to respond differently to sounds of different frequencies High frequencies activate the base (where the stapes vibrates the oval window) and low frequencies activate the apex.

This gives a place code for frequency. This basically sets up labelled lines for each frequency. Neurons activated at the apex code low frequencies; neurons activated at the base code high frequencies.

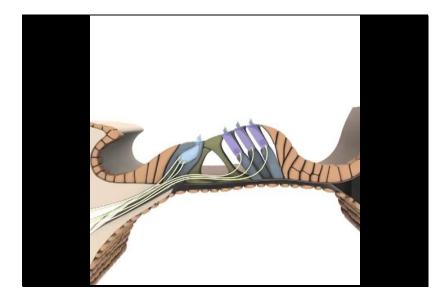


This animation shows how the frequencies of sound are allocated to different places on the basilar membrane

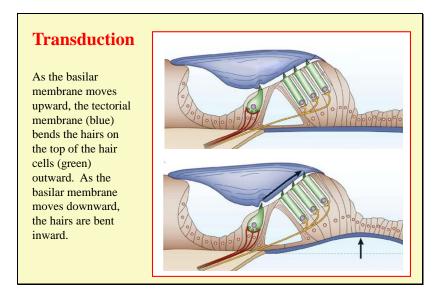
https://www.youtube.com/watch?v=TobHJt1jIHg



The sensory end-organ for hearing, the organ of Corti, rests on the basilar membrane. Alfonso Corti was the Italian anatomist who described the auditory sensory organ in 1851. The cell bodies of the neurons are located around the center of the coiled cochlea – they thus form a spiral ganglion.



This animation lets you a see a section of the moving organ of Corti in three dimensions <u>https://www.youtube.com/watch?v=TF7V6gj9WTI</u>

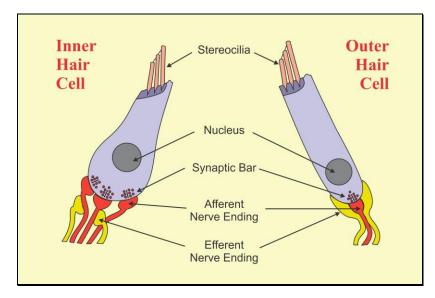


The movement of the basilar membrane causes the tectorial membrane to bend the hairs on top of the hair cells.

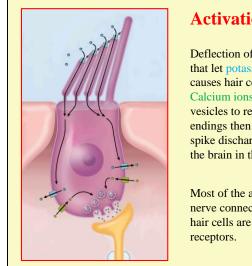
This activates the hair cells which then activate the auditory nerve fibers.

Most of the auditory nerve fibers that conduct information to the brain (afferent - red) are connected to the inner hair cells.

The outer hair cells receive efferent innervation (yellow). They act like little muscles.



This illustration shows the two types of hair cells in the human organ of Corti. Both cells have stereocilia that are in contact with the tectorial membrane. The inner hair cells are the main sensory cells. They respond to the movements of the hairs. Most of the afferent fibers (red) in the auditory nerve come from the inner hair cells. Each afferent fiber comes from only one hair cell. The outer hair cells act like muscles. They contract and relax with the sounds, thereby accentuating the movements of the tectorial membrane. Only a few afferent nerve fibers come from the outer hair cells. Most of the efferent nerve fibers (yellow) in the auditory nerve go to outer hair cells.



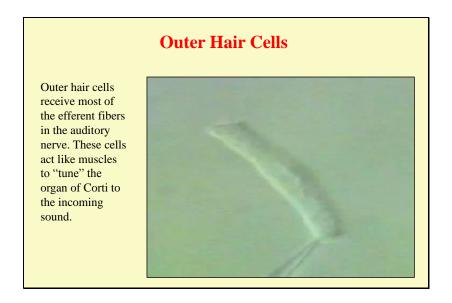
## **Activation of Hair Cells**

Deflection of stereocilia opens channels that let potassium ions into hair cell. This causes hair cell membrane to depolarize. Calcium ions enter cell and cause synaptic vesicles to release transmitter. The nerve endings then depolarize and generate spike discharges which are conducted to the brain in the auditory nerve.

Most of the afferent fibers in the auditory nerve connect to the inner hair cells. Inner hair cells are therefore the main sensory receptors.

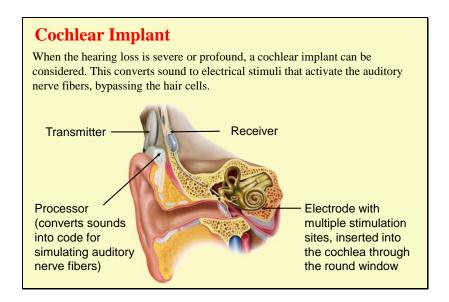
This slide shows the steps involved in activation of the hair cells.

- Bending the hairs in one direction opens channels in the hairs.
- Potassium ions enter the hair cell, changing the membrane potential.
- Calcium-ion channels open letting calcium into the hair cell (green).
- Synaptic vesicles release transmitter (probably glutamate).
- Afferent nerve endings are depolarized and generate action potentials.



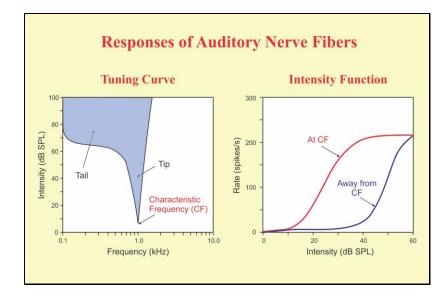
In this video, current is injected into an outer hair cell. The timing of the current follows the music and the external hair cell dances to *Rock Around the Clock* by Bill Haley and the Comets. The movements of the tectorial membrane change the membrane potential. This in turn causes the cell to contract and relax. This accentuates the movements of the tectorial membrane. Video is available at

https://auditoryneuroscience.com/ear/dancing hair cell



If the hair cells are badly damaged but the afferent nerve fibers survive, a cochlear implant can be used to bypass the hair cells and stimulate the nerve fibers directly.

The nerve fibers can be stimulated at multiple locations. This allows the implant to imitate the normal place coding mediated by the traveling wave. High-frequency sounds are sent to electrode locations near to the round window and low-frequency sounds are sent to locations further along the basilar membrane.

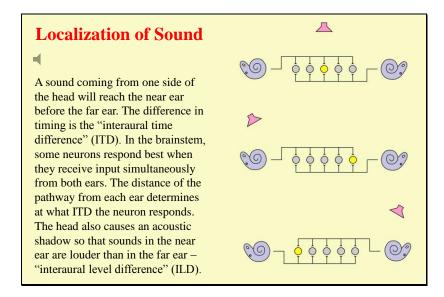


This slide illustrates how auditory nerve fibers respond to sound. The main characteristics of a sound are frequency and intensity.

Frequency is mainly coded by which neurons are active and intensity is mainly coded by how rapidly these neurons discharge. The graph on the left shows the response of a single nerve fiber to sounds of different frequencies. The blue area in the tuning curve indicates the frequencies at which the neuron responds. At low intensities, each auditory fiber responds best at one frequency – the characteristic frequency. At higher intensities it will respond to a range of frequencies but at the lowest intensity it responds only to one.

The frequency of the sound is thus coded by identifying which neurons respond best to that particular frequency. These are activated by hair cells on the basilar membrane at the place where that frequency causes most displacement. The place code of the traveling wave thus becomes a "labelled line" code.

The graph on the right shows the response of a single nerve fiber to a sound of increasing intensity. Intensity is coded by how rapidly the nerve fiber discharges. The rate increases over a range of 30 dB. In order to code a larger range of intensities the central nervous system also has to take into account how many fibers are active.

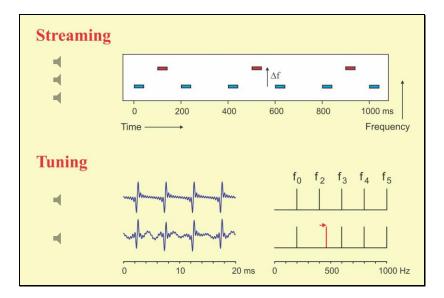


As well as frequency and intensity, a sound is characterized by its location.

A sound coming from one side reaches the ipsilateral ear earlier and with greater intensity than the contralateral ear.

The sound sample is white noise that is earlier on one speaker than the other and then switches its timing back and forth. Heard over earphones the sound moves back and forth between the ears. If only one earphone is used there is just a continuous white noise.

In the auditory brainstem nuclei some neurons compare the relative timing and the intensity of the sound at the two ears.



This slide illustrates two ways that the auditory system distinguishes different auditory "objects." When sounds are relatively close together in frequency, they can be heard as coming from one galloping object.

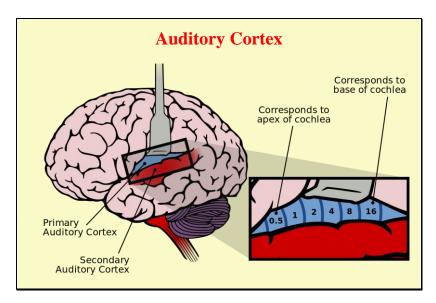
As the sounds move apart in frequency, they become two distinct objects (or sound-streams).

If all the harmonic components of a sound are based on the same fundamental frequency, they are heard as coming from the same source.

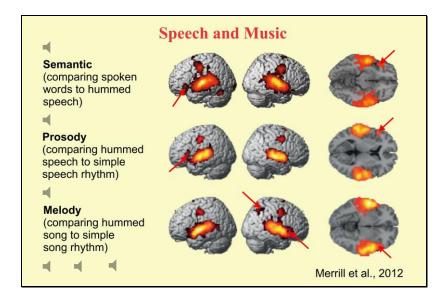
In the first sound sample we hear a buzz.

However, if one harmonic is mistuned, we can hear it as a separate object.

In the second sound sample we hear both a buzz and a tone.



The primary auditory cortex is located on the superior surface of the temporal lobe (blue). On the cortex, the low frequencies are anterior and lateral to the high frequencies.

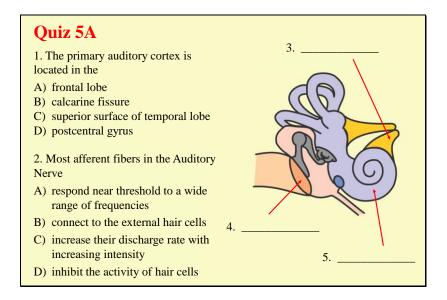


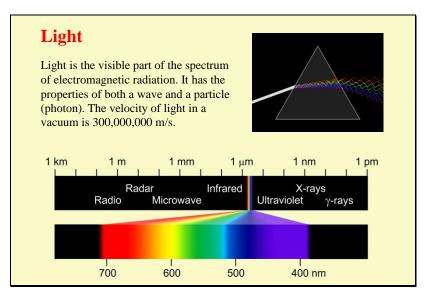
These studies record the blood flow in the brain using functional MRI. The images show the areas of the brain activated when sounds are being heard. The first two images show the left and right hemispheres from the side. The rightmost image shows a cross section with the left at the top and the right at the bottom. The hotter the color the greater the activation. All conditions activate the auditory cortex in the temporal lobe.

"Die Blumen blumen in Marz und Mai am schönsten". Flowers are at their best in March and May.

Listening to words for their meaning also activates the left inferior frontal region (Brocas's area). A similar pattern is seen when listening to the rhythm of speech sounds.

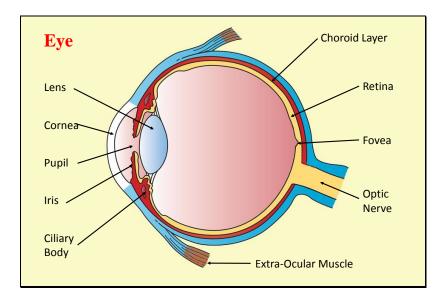
Listening to melody activates the left inferior frontal region in the right hemispheres as well as the right parietal region.





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.

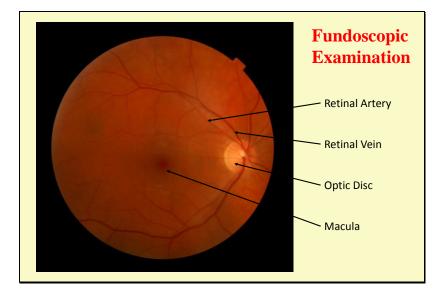
## Human Brain

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  $12-15^{\circ}$  laterally to the center of the visual field.

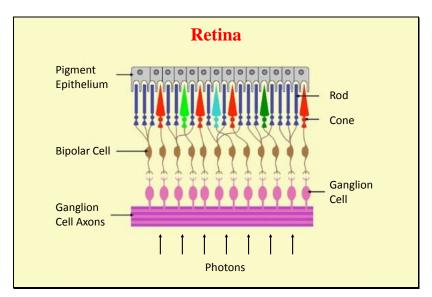
The blue layer is the protective "sclera" (hard). This is continuous with the transparent cornea.



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.

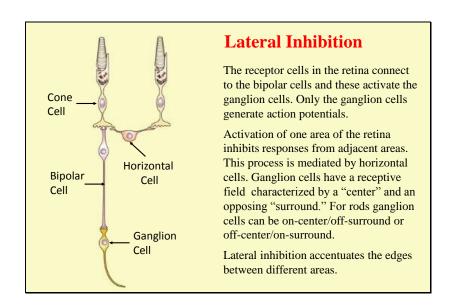
Arteries and veins are in front of the retina.

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. Not in the diagram are the retinal arteries and veins which rest on the ganglion cell layer.

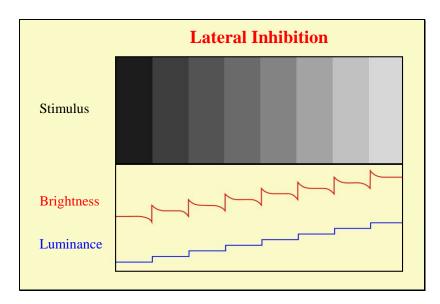


One of the main principles of vision (and indeed of all sensory systems) is "lateral inhibition." Activation of one sensory area inhibits the activity of adjacent areas. In the eye, this inhibition is mainly mediated by the horizontal cells of the retina.

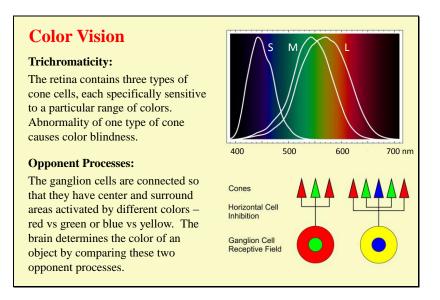
The visual field of a ganglion cell has a center where it is excited (on-center) plus a surrounding region where it is inhibited (off-surround).

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.

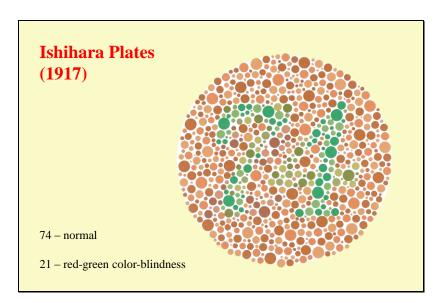


The retina contains three types of cones. (S, M, L mean short medium and long in terms of wavelength).

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

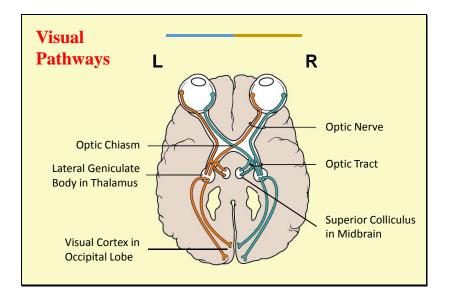
The most common type of colorblindness is an abnormality of the M type of photoreceptor. The subject has difficulty telling red from green. This disorder is determined by an abnormality on the X-chromosome. It is therefore sex-linked recessive. It occur is about 6% of males (and 0.36% of females -0.06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



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.



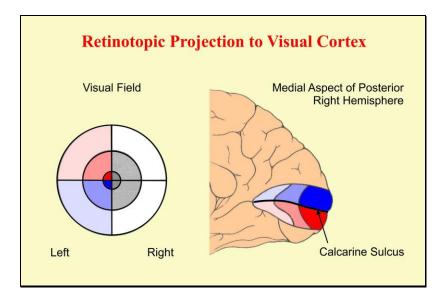
Each eye receives input from both the left and right side of the visual field. Because of the lens the image focused on the retina is reversed – up is down and left is right.

In the diagram on the preceding page, 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.

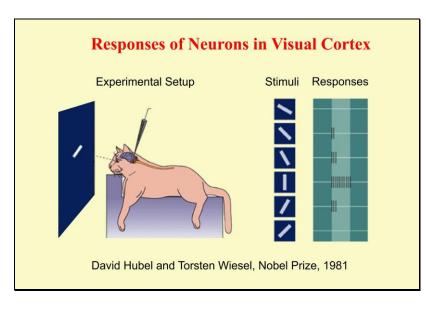
The superior colliculus in the midbrain is a region that helps control eye-movements.



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.

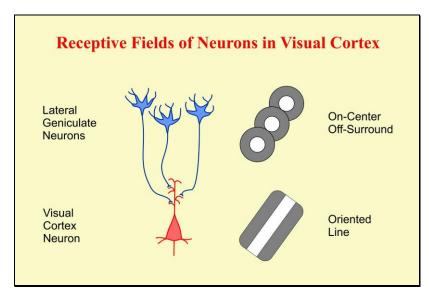


This video shows Hubel and Wiesel mapping the receptive field of a neuron in the cat's visual cortex.

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.

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.

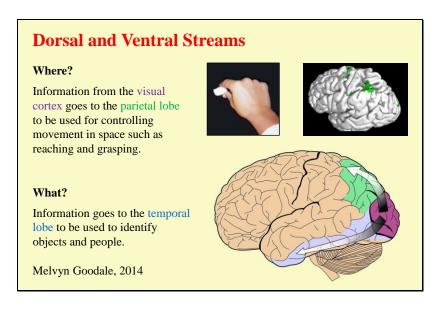
Migraine is a common type of headache.

We do not know its cause but the pain is probably mediated by 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 and visual loss). This is likely triggered by some vascular problem in the visual cortex and spreads from one region to another. One theory is there is a spreading release of potassium ions that excites and then exhausts 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 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=qVFIcF91yk8

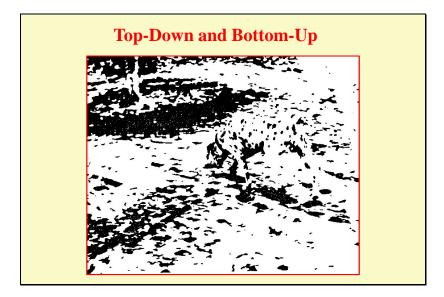


After the visual cortices in the occipital lobe (purple), visual information travels into two different perceptual systems.

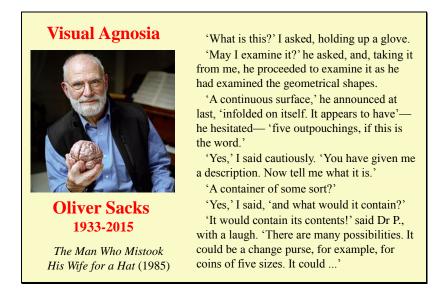
The "where" system in the parietal lobe (green) is used for controlling movements in space. The pictures in the lower right of the slide show the regions of the brain that are active when a small object is being manipulated. These experiments were performed by Mel Goodale and his associates at the University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



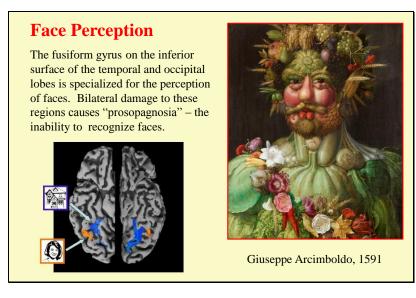
Visual perception combines information coming in from the eyes with expectations and hypotheses about what it might mean. This picture initially looks like a bunch of black dots. However, if we try hard to see things in the picture we can make out a Dalmatian dog rooting about in the leaves. Once we finally see the dog (or if it is pointed out), it becomes obvious.



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

The patient with agnosia can see the 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.

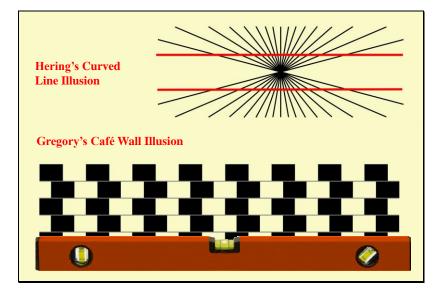
The brain is the same as the plastic brain that I showed you during the first session.



The lower surface of the temporal lobe is specialized for perceiving faces (orange) and objects (blue). 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.

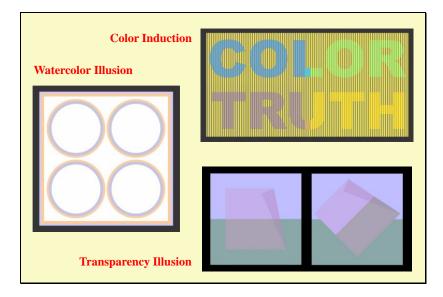


Visual illusions are common. They help us to understand how the visual system works.

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.

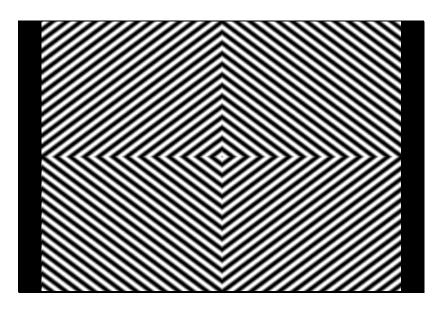


These are some illusions that derive from how we perceive color.

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.

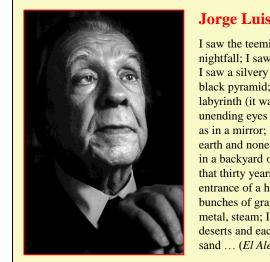


This is an illusion based on perceived movement. It is like the waterfall illusion – staring at a waterfall for a while and then looking at the neighboring rocks or trees will suggest that these stationary objects are rising (motion after-effect).

If you look at this moving 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

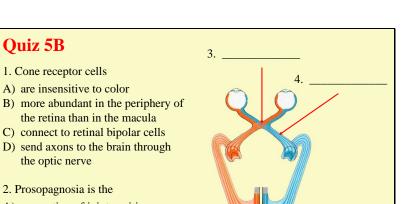
This amazing webpage has many different visual illusions <u>http://www.michaelbach.de/ot/</u>

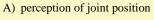


## Jorge Luis Borges (1899-1986)

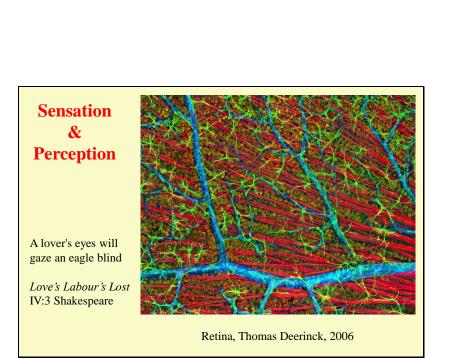
I saw the teeming sea; I saw daybreak and nightfall; I saw the multitudes of America; I saw a silvery cobweb in the center of a black pyramid; I saw a splintered labyrinth (it was London); I saw, close up, unending eyes watching themselves in me as in a mirror; I saw all the mirrors on earth and none 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.





- B) inability to perceive faces
- C) anterior region of the brainD) future course of a disease



This 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.