

Vision, Explained

In this blog post, I'll try to explain the biological vision system, primarily in humans.

How can we understand how vision works?

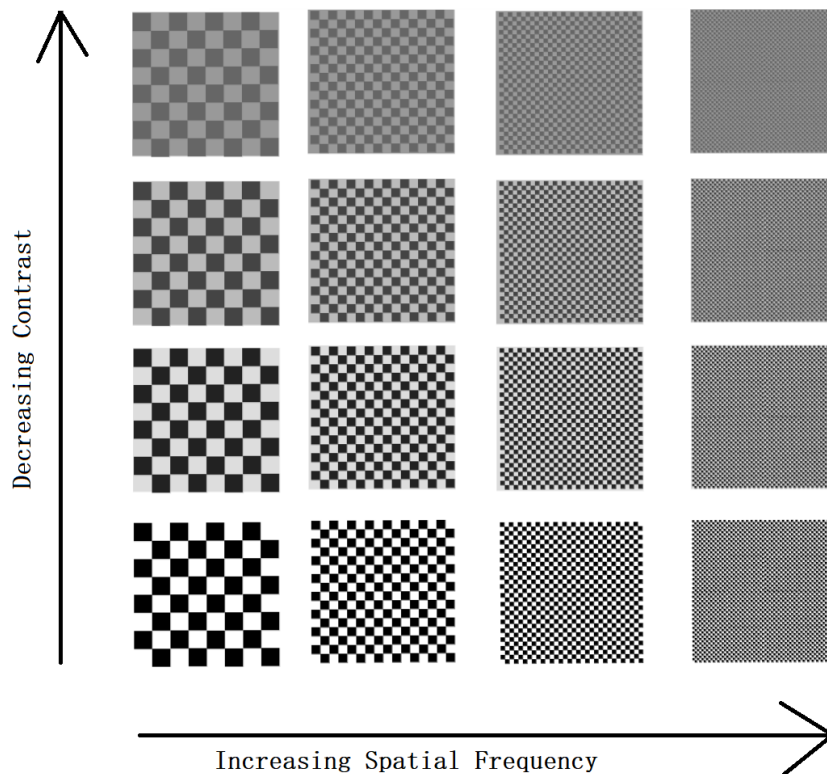
Behavioural Experiments

E	1	20/200
F P	2	20/100
T O Z	3	20/70
L P E D	4	20/50
P E C F D	5	20/40
E D F C Z P	6	20/30
F E L O P Z D	7	20/25
D E F P O T E C	8	20/20
L E F O D P C T	9	
F D P L T C E O	10	
P E Z O L C F T D	11	

Snellen chart, Source: https://en.wikipedia.org/wiki/Snellen_chart

One of the ways to assess visual systems is to run behavioural experiments. While going through an eye-checkup, you probably would have been asked to read some letters on a chart some 20 feet away. That chart is called as the Snellen chart. Reading that chart tells us how well a subject can process fine detail, which is also known by the property of “visual acuity”. Using these experiments, it has been found

that our visual acuity is the highest near central regions of the retina, which means that if you look at the Snellen chart at a side angle (i.e. using peripheral vision), you probably would not be able to figure out those tiny letters that you could figure out when you looked at them straight, centrally. This implies that the visual capacity actually varies with different regions of the visual field.



Another property that researchers try to evaluate is “contrast sensitivity”, which simply means that how well the subject can perceive the changing contrast in an image. A lot of times, spatial frequency alongwith contrast is also tested. To understand this, imagine a chessboard with varying number of squares. More squares per unit of length would mean higher spatial frequency. You can imagine that you would not be able to distinguish between the black and white squares when the spatial frequency goes above a certain value. Changing contrast in this example would mean that instead of presenting pure white and pure black squares, the subjects would be presented with “somewhat white” and “somewhat black” shades of grey.

Understanding the structure of brain parts that perform vision

If you would look at a structural diagram of the brain, you would see various labels in it. You probably have already heard of names like “visual cortex”, “cerebrum”, “cerebellum” etc. A mapping of all the regions of the brain has already been done. Scientists have named different parts of the brain in order to understand their characteristics in more detail. We know which parts are more useful than other parts for vision.

By staining tissues from the brain and visualising them under a microscope, researchers have been successfully able to visualise the structure of even individual neurons. Functional anatomy is a set of techniques through which researchers have been able to visualise the neurons according to their activity values, i.e., highly activated neurons can be made to appear brighter in the visualisation. A popular example of functional anatomy is fMRI or Functional Magnetic Resonance Imaging.

Advanced techniques like two-photon imaging provide much higher spatial resolution than optical microscopy and is used to study cell bodies in fine detail.

Recording and Stimulating Neurons

The electrical activities of neurons can be recorded through really thin electrodes which are known as microelectrodes. They can be made from glass, varnish-coated tungsten, glass-coated platinum-iridium etc. They can take readings from both outside (extracellular) as well as inside (intracellular) the neuron. These recordings have been really helpful in understanding the mechanism of synapses in neurons in detail.

Arrays of microelectrodes can also be used to stimulate multiple neurons simultaneously, using which artificial signals can be produced. A futuristic use-case of this neuronal stimulation can be to replicate images for visually-impaired people. Firstly, the neuronal coding of images would be learned by such a device and then real-time images would be converted into neuronal codes which will be stimulated using an array of microelectrodes.

Understanding the chemical composition of neurons and neurotransmitters

This has been really helpful in understanding how the neurons communicate with each other. The chemical composition is determined

by first isolating the relevant molecules and then using mass spectrometry and gas chromatography techniques.

To understand the functions of neurotransmitters, multiple slightly mutated versions of these molecules are synthesized and then tested to understand their role in communication between neurons.

A common excitatory neurotransmitter in the retina is glutamate while a common inhibitory neurotransmitter is gamma-aminobutyric acid.

Stimulating neurons by light

Many neurons contain compounds known as opsins, that are a group of light-sensitive proteins.

By shining light on these neurons, they can be excited or inhibited depending on the nature of the opsins contained in them. This type of stimulation is known as optogenetic stimulation.

While electrical stimulation generally activates all the neurons in a surrounding tiny area around the electrode tip, optogenetic stimulation is opsin-specific and only activates those neurons which contain the target opsin.

Blocking brain areas

Researchers have been studying visual capacities of humans whose brain parts were damaged because of accidents and other causes like war combats.

Animal brains have also been extensively studied, in which parts of their brains have been surgically removed or made nonfunctional by subjecting them to extremely cold temperatures.

Instead of blocking entire brain regions, specific sets of neurons and neurotransmitters can also be blocked by infusing certain substances.

This technique helps researchers understand the functionality of various brain regions and neurotransmitters.

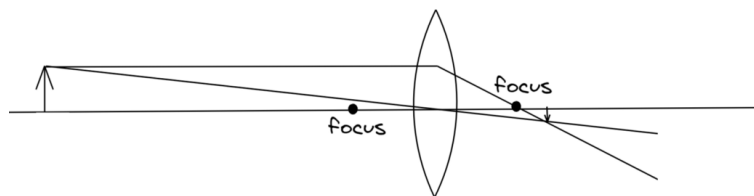
How is our visual system wired?

The lens in the eye

For cameras, the distance between the recording surface at the back of the camera and the lens is varied in order to focus on objects in images. The glass lens' thickness is fixed in almost all cameras. In some species like octopus, this is exactly what happens. The lens' thickness is constant and it's moved back and forth from the fovea in order to focus suitably.

But in many species like humans, our lenses in our eyes can be made thicker or thinner by the help of some muscles, through which we appropriately focus on objects in the visual scene. This flexibility decreases with age in humans.

Everything we see actually forms an inverted image on the retina.



Formation of inverted image through a convex lens when object is placed anywhere beyond the focal length. The maximum focal length of the human eye is around 25 mm.

Why are most pupils black in colour?

Except for the central region (the fovea) where visual acuity is the highest, most of the photons pass through several layers of cells in the retina before they strike the photoreceptors. These layers contain a black pigment because of which the pupils appear black in most individuals. This black pigment absorbs the incoming light which would have otherwise reflected and scattered in multiple directions and would have activated multiple photoreceptors, which would have greatly decreased our visual acuity. This inference is supported by the fact that albinos, who don't have this black pigment epithelium, have very poor visual acuity.



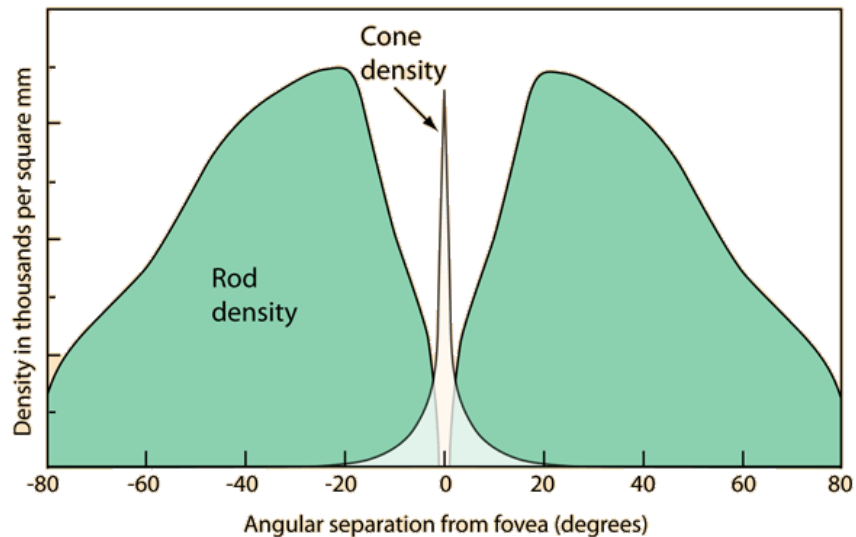
Most pupils are black in colour; Source: <http://www.daltonism.org.uk/2018/04/human-eye-color/>

In some animals like deers, however, this pigment epithelium instead of absorbing the light, is reflective in nature, thereby enabling them to see better in low-illumination conditions.



Eyes of deer at night; Source:
<https://www.northcountrypublicradio.org/news/story/12526/20180315/what-makes-some-eyes-shine-at-night>

| *Photoreceptors in the eye*



Source: <http://hyperphysics.phy-astr.gsu.edu/hbase/vision/rodcone.html>. Distribution of photoreceptors in humans. Note that right at the fovea, there aren't any rod cells present.

There are two different types of photoreceptors in the eye: the rods and the cones. It was found that the fovea region contained no rod cells and also that night vision in fovea is low. This implied that rod cells are responsible for low-light vision. The distribution of photoreceptors in mice is quite uniform but in higher level species like cats and primates, this distribution is quite non-uniform. It is believed that this happened because a uniform distribution of highly dense photoreceptors would have required a lot of energy and we would need to eat as much food as an elephant to survive. Instead, we developed the ability to move our eyes quickly so that we could direct our fovea region at different parts of the visual scene and look at it from multiple views.

Why our eyes are not at the sides of our heads like birds, fishes and amphibians?

Eyes at the sides of the head provide access to a larger visual field at once. But we have both our eyes at the front, due to which the region which is seen by both eyes (binocular overlap) increases, and the range of the visual field decreases. The advantage that we get with this binocular overlap is that of depth perception. By figuring out the subtle differences between images formed by the same object in both the eyes, our brains could figure out how close or how far it is from us. Many species of birds have two foveae in each eye through which they estimate depth.



Fishes have eyes at the sides of their heads while apes have both eyes at the front; Sources: <https://www.thesprucepets.com/pop-eye-symptoms-and-cure-1379917> (left) and <https://news.st-andrews.ac.uk/archive/the-eyes-have-it/> (right)

About membrane potential of the neuron

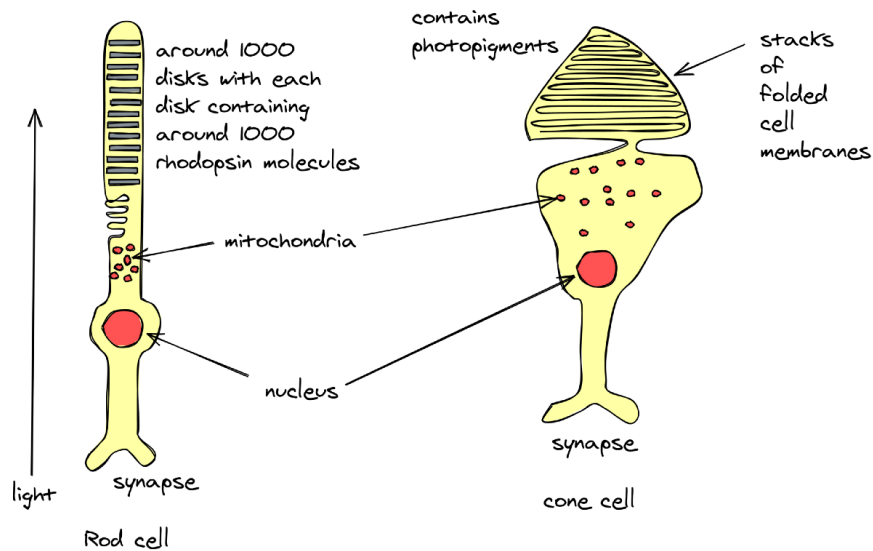
In resting state, the inner wall of the membrane of a neuron is at a lower potential than its outer wall. If the outer wall potential is kept at zero, the inner wall is typically at -70 mV in the resting state. This is called as the resting membrane potential difference of the neuron. If this potential difference becomes more negative, then we say that the neuron has become hyperpolarized (because it moves away from zero), otherwise we say that it has depolarized (because it moves closer to zero).

An action potential (a spike) takes place when the neuron depolarizes beyond a threshold (-55 mV typically). Typically one expects that some stimulus would depolarize the neuron that would cause an action potential resulting in an action potential in the next neuron and so on.

The Retina

There are five major classes of cells present in the retina, namely, the photoreceptors (rods and cones), the retinal ganglion cells, the bipolar, horizontal and amacrine cells. We'll discuss the photoreceptors and the retinal ganglion cells here.

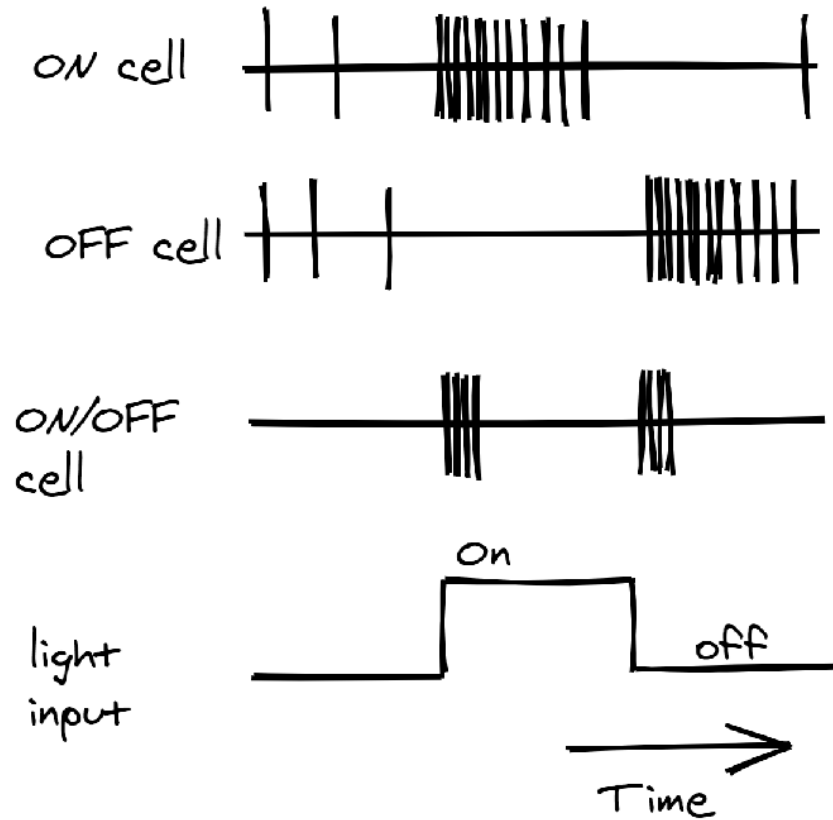
The Photoreceptors



structures of rod and cone cells

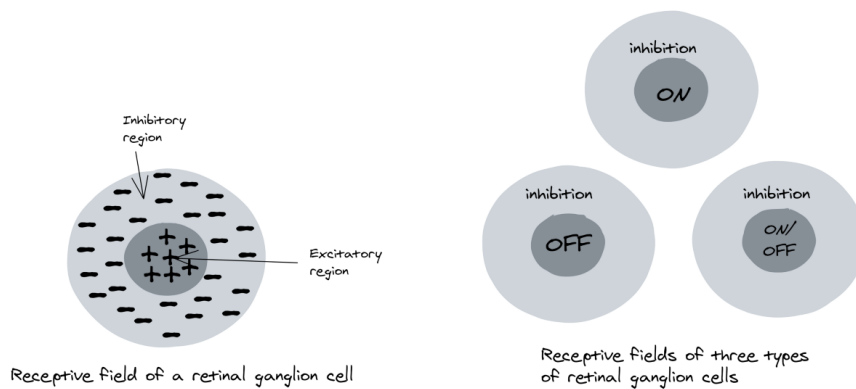
The incoming light in the rod cells photobleach the rhodopsin molecules, causing hyperpolarization of the rod cell. Interestingly, the disks in these rods are created at one end and discarded at the other. Typically, one new disk is created and discarded daily, in humans. We have three types of cone cells, sensitive to red, green and blue wavelengths. The blue cone cells are the lowest in number, but they have the highest sensitivity. Also, rods and cones near the fovea are much tinier than rods and cones in the periphery.

Retinal Ganglion Cells



The three major types of retinal ganglion cells as discovered in the 60s

It was found in the 60s that, majorly, there are three types of retinal ganglion cells—the ON cells, the OFF cells and the ON/OFF cells. The ON cells fired when the light entered the eye, the OFF cells fired when the light was stopped and the ON/OFF cells fired whenever the mode switched from ON to OFF or vice versa. It was also found that these cells are responsive to very small part of the visual field, which is called as the receptive field of the cell.



Also when light was shined in proximity to the centre of the receptive field, the response was very strong but when light was shined to the entire receptive field, the response was weak. This inferred that there

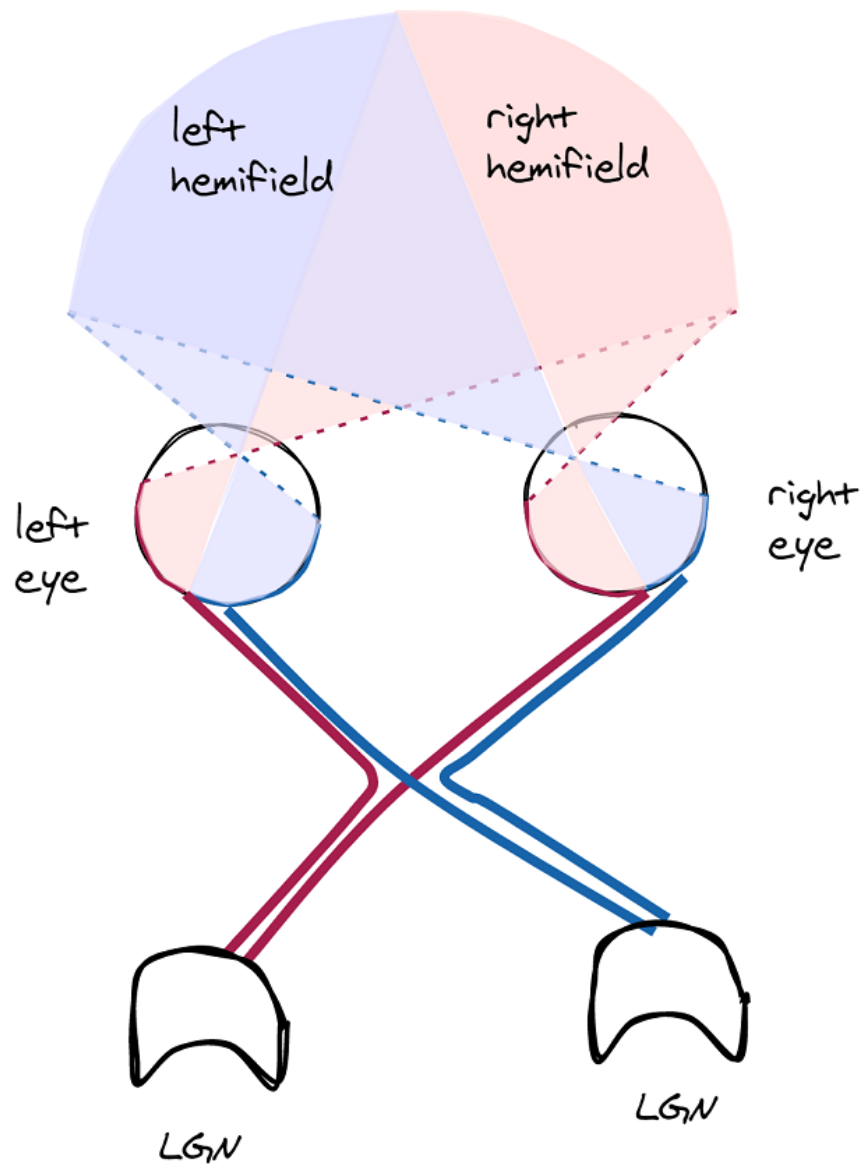
was also some kind of inhibitory response present in the receptive field of the cell. It was discovered that the retinal ganglion cells have an excitatory centre surrounded by an inhibitory region, as shown in the above figure.

There are other ways in which one can classify retinal ganglion cells, like on the basis of their sizes, their projections and the conduction velocities of their axons.

How does information transmit from the photoreceptors to the retinal ganglion cells?

Surprisingly, the presence of light hyperpolarizes (rather than depolarizing) the photoreceptors. They only produce transient local changes in their membrane potentials which are called as graded potentials. These graded potentials cause changes in neurotransmitter release in the postsynaptic neurons. All horizontal cells which are connected to the photoreceptors also hyperpolarize to light. But some bipolar cells hyperpolarize and some depolarize to light (that's where the ON and OFF nature comes in). But they also only give graded potentials. Some amacrine cells do give action potentials. And lastly, all retinal ganglion cells generate action potentials.

| *Wiring from the retina to the lateral geniculate nucleus*



Wiring of the visual system from the retinae to the lateral geniculate nuclei (LGNs)

Each retina can be divided into two parts, the temporal part and the nasal part. The nasal part is the part which is closer to the nose (i.e. in the middle), and temporal is the other part. So, the nasal part of the left eye and the temporal part of the right eye look at the images from the left hemifield (shown in blue), while the temporal part of the left eye and the nasal part of the right eye look at the images from the right hemifield (shown in red).

The lateral geniculate nucleus (LGN) is a relay center between the visual cortex and the retinal cells, which of course, receives inputs from the retina, but more interestingly, it also has many feedback connections from the visual cortex which helps in the functioning of the top-down attention system. Geniculum in Latin means a small knee joint. The LGN is named so because of its resemblance in shape to a

bent knee. The inputs which capture the left hemifield project to the right LGN and those which capture the right hemifield project to the left LGN.