THE EYE

by the book David Hubel's "Eye, Brain and Vision".

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The collective function of the nonretinal parts of the eye is to keep a focused, clear image of the outside world on the two retinas.

Each eye is positioned in its socket by the six small extraocular muscles; they consist of three pairs, with the muscles in each pair working in opposition, so as to take care of movements in one of three orthogonal planes.

For both eyes, the job of tracking an object has to be done with a precision of a few minutes of arc – or else we see double. Such precise movements require a collection of finely tuned reflexes, including those that control head position.

The cornea (the transparent front part of the eye) and **lens** together form the equivalent of the camera lens.
About two-thirds of the bending of light necessary for focusing takes place at the air–cornea interface, where the light enters the eye.
The lens of the eye supplies the remaining third of the focusing power, but its main job is to make the necessary adjustments to focus on objects at various distances.
We focus our eye not by changing the distance between lens and retina but by changing the shape of the rubbery, jellylike lens - by pulling or relaxing the tendons that hold it at its margin - so that it goes from more spherical for near objects to flatter for far ones.
A set of radial muscles called **ciliary muscles** produces these changes in shape.

Two other sets of muscles change the diameter of the pupil and thus adjust the amount of light entering the eye, just as the iris diaphragm of a camera determines the f-stop.
One set, with radial fibers like the spokes of a wheel, opens the pupil; the other, arranged in circles, closes it.

Finally, the self-cleaning of the front of the cornea is achieved by blinking the lids and lubricating with tear glands.

The cornea is richly supplied with nerves subserving touch and pain, so that the slightest irritation by dust specks sets up a reflex that leads to blinking and secreting of more tears.

The **retina** translates light into nerve signals, allows us to see under conditions that range from starlight to sunlight, discriminates wavelength so that we can see colors, and provides a precision sufficient for us to detect a human hair or speck of dust a few meters away.

The retina is part of the brain, having been sequestered from it early in development but having kept its connections with the brain proper through a bundle of fibers - the optic nerve.

The retina has the shape of a plate about a quarter millimeter thick. It consists of three layers of nerve - cell bodies separated by two layers containing synapses made by the axons and dendrites of these cells.
The tier of cells at the back of the retina contains the light receptors, the **rods** and **cones**.

Rods, which are far more numerous than cones, are responsible for our vision in dim light and are out of commission in bright light.

Cones do not respond to dim light but are responsible for our ability to see fine detail and for our color vision.

The numbers of rods and cones vary aloud over the surface of the retina.

In the very center, where our fine-detail vision is best, we have only cones. This rod-free area is called the **fovea** and is about half a millimeter in diameter.

Cones are present throughout the retina but are most densely packed in the fovea.

Because the rods and cones are at the back of the retina, the incoming light has to go through the other two layers in order to stimulate them.
As it is, the layers in front of the receptors are fairly transparent and probably do not blur the image much.
In the central one millimeter, however, where our vision is most acute (the consequences of even slight blurring would be disastrous), one can see that the other layers displaced to the side to form a ring of thicker retina, exposing the central cones so that they lie at the very front.
The resulting shallow pit constitutes the fovea.

The middle layer of the retina (between the rods and cones and the retinal ganglion cells) contains three types of nerve cells: bipolar cells, horizontal cells, and amacrine cells.

Bipolar cells receive input from the receptors and many of them feed directly into the retinal ganglion cells.

Horizontal cells link receptors and bipolar cells by relatively long connections that run parallel to the retinal layers.

Amacrine cells link bipolar cells and retinal ganglion cells.

The layer of cells at the front of the retina contains the retinal **ganglion cells**, whose axons pass across the surface of the retina, collect in a bundle at the optic disc, and leave the eye to form the optic nerve.

Each eye contains about 125 million rods and cones but only 1 million ganglion cells.

- How detailed visual information can be preserved.

Studying the connection between cells in the retina can help resolve this problem.
One can think of the information flow through the retina as following two paths:
a **direct path**, from light receptors to bipolar cells to ganglion cells, and
an **indirect path**, in which horizontal cells may be interposed between the receptors and bipolars, and amacrine cells between bipolars and retinal ganglion cells.

The direct path is compact, i.e. one receptor or few feed into a bipolar cell, and only one or few bipolars feed into a ganglion cell.
The indirect path is more diffuse, or extended, through wider lateral connections.
The total area occupied by the receptors in the back layer that feed one ganglion cell in the front layer, directly and indirectly, is only about one millimeter.

That area is called the **receptive field** of the ganglion cell – the region of retina over which one can influence the ganglion cell's firing by light simulation.

In and near the fovea (where our ability to make out fine detail is highest) we have the direct path, i.e. a single cone feeds a single bipolar cell, and a single bipolar feeds into one ganglion cell.

On the periphery (where vision becomes relatively crude) we have the indirect path, i.e. more receptors converge on bipolars and more bipolars converge on ganglion cells.

This high degree of convergence, which we find over much of the retina, together with the very compact pathway in and near the very center, helps to explain how there can be a 125:1 ratio of receptors to optic nerve fibers without our having hopelessly crude vision.

Describe the output of the retina - represented by the activity of the ganglion cells.

With a steady, diffuse background light, or even in utter darkness, most retinal ganglion cells kept up a steady, somewhat irregular firing of impulses, at rates of from 1 to 2 up to about 20 impulses per second.

There are two types of the ganglion cells: on-center cells and off-center cells.

An **on-center cell** discharge at a markedly increased rate when a small spot turns on anywhere within a well-defined area in or near the center of the receptive field.

If you listen to the discharges of such a cell, you will first hear spontaneous firing, perhaps an occasional click, and then, when the light go on, you will hear a barrage of impulses that sounds like a machine gun firing.

We call this form of response an **on–response**.

If move the spot of light a small distance away from the center of the receptive field, one can discover that the light suppress the spontaneous firing of the cell, and that when we turn off the light the cell give a brisk burst of impulses, lasting about 1 second. We call this entire sequence an **off–response**.

The receptive field cleanly subdivide into a circular on–region surrounded by a much larger ring-shaped off–region.

Maximal on–responses one can obtain to just the right size circular spot, and maximal off–responses to a ring of just the right dimensions (inner and outer diameters).
The center and surround regions interact in an antagonistic way: the effect of a spot in the center is diminished by shining a second spot in the surround.
The most impressive demonstration of this interaction between center and surround occur when a large spot cover the entire receptive field of ganglion cell.
This evoke a response that is much weaker than the response to a spot just filling the center.

An **off-center cell** have the opposite behavior.
Its receptive field consist of a small center from which off–responses are obtained, and a surround that give on–responses.
The two kinds of cells are intermixed and seem to be equally common.
An off-center cell discharges at its highest rate in response to a black spot on a white background, because we are now illuminating only the surround of its receptive field.
In nature, dark objects are just as common as light ones, which may help explain why information from the retina is in the form of both on-center cells and off-center cells.

If you make a spot progressively larger, the response improves until the receptive-field center is filled, then it starts to decline as more and more of the surround is included.

With a spot covering the entire field, the center either just barely wins out over the surround, or the result is a draw.

The term receptive field refers to the specific receptors that feed into a given cell in the nervous system, with one or more synapses intervening.
Speaking of "mapping out a cell's receptive field", we often mean not simply separating its boundaries on the retina or at the screen, but also describing the substructure i.e. an account of how you have to stimulate an area to make the cell respond.

The map of the receptive field of a cell is a powerful and convenient shorthand description of the cell's behavior, and thus of its output.

- What a population of cells such as the output cells of the retina, are doing in response to light?

Two ways of decision.

- How we need to stimulate to make one cell respond;
- How some particular retinal stimulus affects the entire population of ganglion cells.

Neighboring retinal ganglion cells receive their inputs from richly overlapping and usually only slightly different arrays of receptors.

The cell colored purple and the one colored blue receive inputs from the overlapping regions, shown in cross section. Because one cell makes synapses with many others at each stage, one receptor can influence hundreds or thousands of ganglion cells.
It will contribute to the receptive-field centers of some cells and to the surrounds of others. It will excite some cells, through their centers if they are on–center cells and through their surrounds if they are off–center cells; and it will similarly inhibit others, through their centers or surrounds.
Thus a small spot shining on the retina can stir up a lot of activity, in many cells.

Obviously our vision completely depends on information the brain receives from the eyes; all this information is conveyed to the brain by the axons of retinal ganglion cells.
Fineness of detail is best measured not by the overall size of receptive fields, but by the size of the field centers.
We can describe the size of a receptive field in two ways:

- Give a description its size on the retina;
- Express receptive-field size as the angle subtended by the receptive field on the screen.

One can calculate this angle in radians simply by dividing the field diameter by the screen distance or in degrees: (radians x 180)/π.
One millimeter on the human retina corresponds to an angle of about 3.5 degrees.
At 135 centimeters screen distance, 2.5 centimeters on the screen corresponds to 1 degree. The moon and sun, seen from the earth, are about the same size, and each subtends one–half a degree.

In the fovea, cones have diameters and center-to-center spacing of about 2.5 micrometers, a figure that matches well with our visual acuity, measured in terms of our ability to separate two points as close as 0.5 minutes of arc.
A circle 2.5 micrometers in diameter on the retina (subtending 0.5 minutes) corresponds to a quarter viewed from a distance of about 150m.
Far out in the periphery of the retina, receptive-field centers are made up of thousands of receptors and can have diameters of degree or more.

Thus as we go out along the retina from its center, three items correlate in an impressive way, surely not by coincidence: visual acuity falls, the size of the receptor population contributing to the direct pathway (from receptors to bipolars to ganglion cells) increases, and the sizes of receptive-field centers increase.

The center of the receptive field is determined by the direct path and the antagonistic surround by the indirect one, and the direct path sets limits on our acuity.

Rods and cones differ in a number of ways:

- in their relative sensitivity: rods are sensitive to very dim light, cones require much brighter light.
- in their distribution throughout the retina, there are no rods in the fovea.
- in shape: rods are long and slender; cones are short and tapered.

Both rods and cones contain light-sensitive pigments.

All rods have the same pigment; cones are of three types, each type containing a different visual pigment.

The four pigments are sensitive to different wavelengths of light, and in the case of the cones these differences form the basis of our color vision.

The receptors respond to light through a process called **bleaching**.

In this process a molecule of visual pigment absorbs a photon and is thereby chemically changed into another compound that absorbs light less well, or perhaps differs in its wavelength sensitivity.

Most ordinary sensory receptors - chemical, thermal, or mechanical - are depolarized in response to the appropriate stimulus, just as nerves become depolarized in response to an excitatory stimulus; the depolarization leads to release of transmitter at the axon terminals.

It was assumed (up to 1964) that a similar mechanism - depolarization in response to light - would hold for (vertebrate) rods and cones. But it is not true!

In the dark, vertebrate light receptors are apparently more depolarized (and have a lower membrane potential) than ordinary resting nerve cells, and the depolarization causes a steady release of transmitter at the axon terminals, just as it would in a conventional receptor during stimulation.

Light, by increasing the potential across the receptor-cell membrane (i.e., by **hyperpolarizing** it), cuts down this transmitter release.

Stimulation thus turns the receptors off, strange as that may seem.

Therefore the optic-nerve fibers of vertebrates are so active in the dark.

In 1970 the flow of ions in the dark, or **dark current**, was discovered.
It causes depolarization of the receptor at rest, and hence its continual activity.

As a result of the bleaching of the visual pigment in response to light, the dark current decreases, and the membrane depolarization declines-the cell thus hyperpolarizes. Its rate of activity (that is, transmitter release) decreases.

All this makes it possible to explain several previously puzzling phenomena:

- a fully dark-adapted human can see a brief flash of light;
- the inability of rods to respond to changes in illumination if the light is already bright.

Horizontal cells and bipolar cells occur, along with amacrine cells, in the middle layer of the retina.

The bipolar cells are a part of both the direct and indirect paths. In contrast, horizontal cells are a part of the indirect path only.

Horizontal cells are much less numerous than bipolar cells.

The bipolar cells have also center-surround receptive fields, as ganglion cells, and come in two types, on–center and off–center.

The center is supplied by direct input from a small group of receptors; the surround arises from an indirect path stemming from a wider expanse of receptors that feed into horizontal cells, which feed into the bipolars.

For the off-center bipolars the synapses from the receptors must be excitatory, because the receptors themselves are turned off (hyperpolarized) by light; for the on-center bipolars the synapses must be inhibitory.

Horizontal cells are large cells and come in several subtypes.

Unusual features:

• their lack of anything that looks like an ordinary axon. The processes that come off the cell bodies of horizontal cells (and amacrine cells) serve the functions of both axons and dendrites;

• the synapses that horizontal cells make with receptors, lacking the electron-microscopic features that would normally tell us which way the information is conveyed.

Horizontal cells get their input from receptors; their output is still uncertain, but is either back to receptors, or to bipolar cells, or to both.

The receptive fields of horizontal are large. They are uniform, giving hyperpolarization wherever you stimulate, and more hyperpolarization the larger the spot.

When horizontal cells connect directly to bipolars, the synapses to on-bipolars would have to be excitatory and those to off-bipolars, inhibitory. If the influence is by way of the receptors, the synapses would have to be inhibitory.

These cells come in an amazing variety of shapes and use an impressive number of neurotransmitters.
They all have in common:
• their location, with their cell bodies in the middle retinal layer and their processes in the synaptic zone between that layer and the ganglion cell layer;
• their connections, linking bipolar cells and retinal ganglion cells and thus forming an alternative, indirect route between them;
• their lack of axons, compensated for by the ability of their dendrites to end presynaptically on other cells.

Amacrine cells have several different functions, many of them unknown.

One type of amacrine play a part in specific responses to moving objects; another type is interposed in the path that links ganglion cells to those bipolar cells that receive rod input.

The synapses between bipolar cells and ganglion cells are all excitatory, and this means that **on-center bipolar cells supply on-center ganglion cells, and off-center bipolars supply off-center ganglion cells**. That simplifies the circuit!

In 1976 it was established that, in the direct pathway, it is the off-center system that has excitatory synapses at each stage, from receptors to bipolars and bipolars to ganglion cells. The on-center path instead has an inhibitory receptor-to-bipolar synapse.

The separation of bipolar cells and ganglion cells into on- and off-center categories have perceptual correlates.

Off-center cells respond in exactly the same way to dark spots as on-center cells respond to bright spots.

Thus there are separate sets of cells for handling dark and light spots. Black is as real to us as white, and just as useful.

Similarly, situation occurs in the realm of heat and cold. From physics we know that cold is just the absence of heat, but cold seems equally real.

It is true, because we have two classes of temperature receptors in our skin, one that responds to the raising of temperature, and another to lowering. So again, biologically, cold is just as real as hot.

Many sensory systems make use of opposing pairs: hot/cold, black/white, head rotation left/head rotation right, yellow/blue and red/green.

- For what need the center-surround receptive fields? What use they are to us?

The messages that the eye sends to the brain have little to do with the absolute intensity of light shining on the retina, because the retinal ganglion cells do not respond well to changes in diffuse light.

What the cell does signal is **the result of a comparison of the amount of light hitting a certain spot on the retina with the average amount falling on the immediate surround.**

The cell's failure to respond well to anything but local intensity differences may seem strange, because when we look at a large, uniformly lit spot, the interior seems as vivid to us as the borders.

The ganglion cell reports information only from the borders of the spot;
we see the interior as uniform because no ganglion cells with fields in the interior are reporting local intensity differences.

This system carries another major advantage in addition to efficiency.
We see most objects by reflected light, from sources such as the sun or a light bulb.

Despite changes in the intensity of these sources, our visual system preserves to a remarkable degree the appearance of objects.
The retinal ganglion cell works to make this possible.

One can measure the light coming to our eyes from the white paper and from one of the black letters.

	Outdoors	Room
White paper	120	6.0
Black letter	12	0.6

The light outside is evidently twenty times as bright as the light in the room, and the black letters reflect about one–tenth the light that white paper does.

Clearly, the appearance of black and white is not a function of the amount of light an object reflects.
The important thing is the amount of light relative to the amount reflected by surrounding objects.

"Black" and "white" are more than physical concepts; they are biological terms, the result of a computation done by our retina and brain on the visual scene.

This situation (for "black" and "white") is the same for color. The color of an object is determined not just by the light coming from it, but also - as in the case of black and white - by the light coming from the rest of the scene.

As a result, what we see becomes independent not only of the intensity of the light source, but also of its exact wavelength composition.

And again, this is done in the interests of preserving the appearance of a scene despite marked changes in the intensity or spectral composition of the light source.