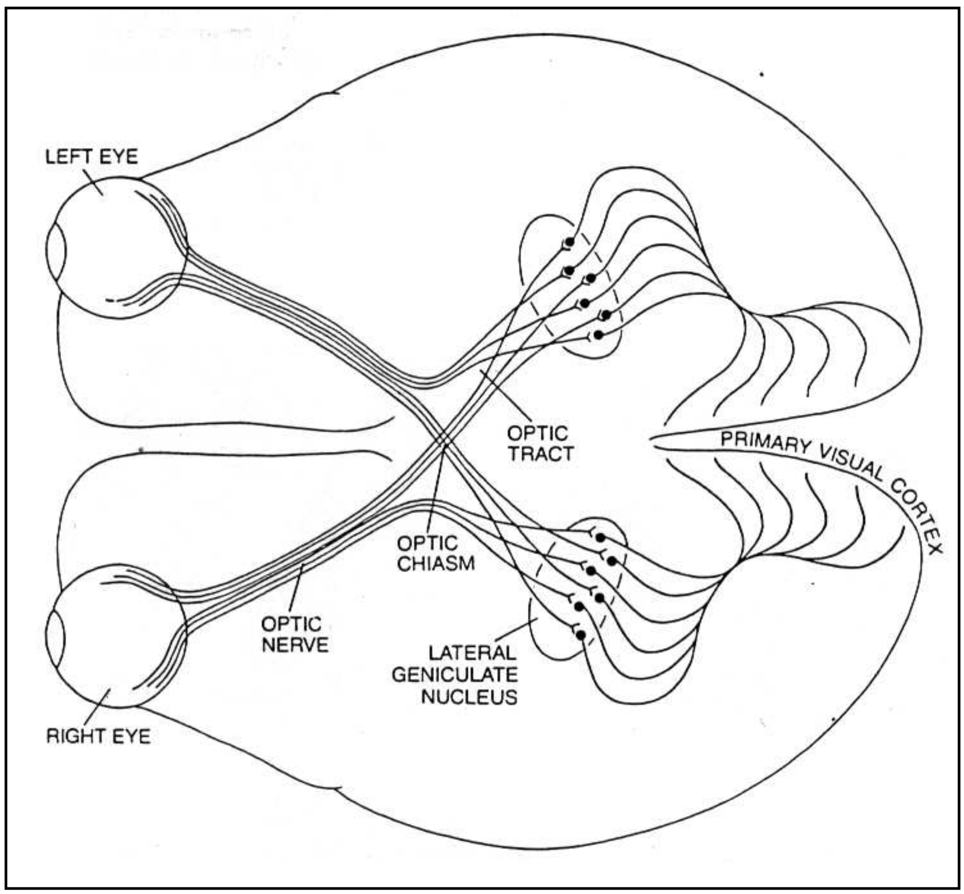
A lot of what is known about vision today came to us through the work of scientists in the 1960s performing experiments on monkeys. These experiments involved inserting electrodes in the subjects' brains in order to measure the response to light stimuli on the retina at various intensities, locations, and shapes. This experimentation has had successes in mapping the process of vision from the eye to the primary visual cortex at the back of the brain.

It must be realized that this information is only barely scratching the surface of visual processing and perception in the brain. Consider that for each connection feeding forward from the eye into the brain, there are roughly five feedback connections.

The retina

Light entering the eye is focused by the lens and forms an inverted image on the retina, which is the thin light-sensitive layer coating the inside of the back of the eye. The retina itself is highly structured and layered. It should be noted that the right side of the visual world forms an image on the left side of each retina, and vice versa.

The light-sensitive structures on the back of the retina are the rods and cones. Rods are sensitive to light intensity, while cones are sensitive to wavelength. It can be roughly said that there are three kinds of cones, each sensitive to one of red, blue, and green light. Because of practical constraints, this course will only be dealing with analyzing light-intensity images, so the cones are somewhat irrelevant.



The optic nerve and the lateral geniculate nucleus

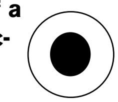
Each retina feeds input into an optic nerve, which itself is a bundle of ganglion (clustered) cell axons (nerve cell endings). It is interesting to note that the spot on the retina which connects to the optic nerve is 'blind,' that is, no image can be formed there. Recalling that the left part of the visual world forms an inverted image on the right side of each retina, it is logical that each optic nerve-bundle splits and partially intersects with the other at the optic chiasm, so the inputs from each eye on one particular half of the visual world can be processed together. The ganglion-cell axons feed input into two nests of cells deep in the brain called the lateral geniculate nuclei (LGN). The LGN axons feed directly into the primary visual cortex.

Receptive fields

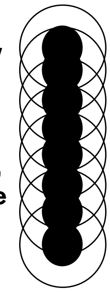
It is appropriate at this point to introduce the abstract concept of a receptive field. The firing rate of each retinal ganglion, geniculate, and cortical neuron can be thought of as a function of the intensity of light on certain areas of the retina. It is convenient to generalize these small patches on the retina as a cells' respective field. The receptive field of both a retinal ganglion and geniculate cell can be characterized as having a sort of circularly symmetric, centre-surround configuration - “an excitatory centre and an inhibitory surround” (Hubel and Wiesel), or the opposite arrangement. All of these cells respond to stimuli in only one eye.

In the cortex, there is a hierarchy of cells feeding others with receptive fields of increasing complexity. Hubel and Wiesel’s overview of the different types the receptive fields in the cortex is quite good: “The simplest, which we call “simple” cells, behave as though they received their input directly from several cells with centre-surround, circularly symmetrical fields....The response properties of these simple cells, which respond to an optimally oriented line in a narrowly defined location, can most easily be accounted for by requiring that the centres of the incoming centre-surround fields all be excitatory or all be inhibitory, and that they lie along a straight line....The second major group of orientation-specific neurons are the far more numerous “complex” cells...their main feature is that they are less particular about the exact position of a line....Complex cells behave as though they received their input from a number of simple cells, all with the same receptive-field orientation but differing slightly in the exact location of their fields.” Additionally, it is only at the level of complex cells that input from both eyes begins to be processed together. In these binocular cells, the receptive field has an identical configuration for both eyes; however, results obtained by testing each eye separately with identical stimuli are usually not quantitatively identical. That is, each cell usually has some sort of ocular preference to stimuli in one of the left or right eye in particular. Complex cells respond best to specifically-oriented line segments – a change in orientation of 10 or 20 degrees from the optimal orientation is likely to markedly reduce or abolish the response in a particular complex cell.

A receptive field representation of a ganglion or geniculate cell, with a centre-surround, circularly symmetric configuration. Black marks excitatory areas; white marks inhibitory areas.

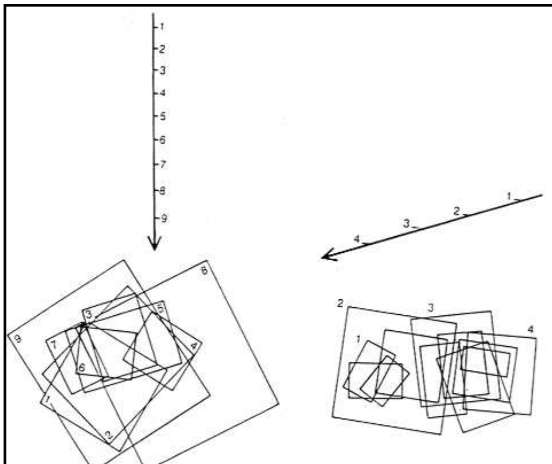


An example of how a number of ganglion/geniculate cells can feed one simple cortical cell, with a net receptive field that is a straight line



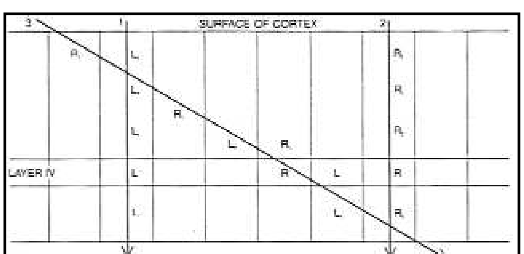
The primary visual cortex

The primary visual cortex (PVC) is a layered area covering 15 square centimetres of the highly-folded cerebral cortex, onto which the visual world is mapped. Layer IV of the PVC is connected directly to the lateral geniculate nucleus, from which it receives input. The cells low in layer IV have a centre-surround configuration similar to the retinal ganglion and geniculate cells, and the simple cells described above lie just above the centre-surround cells from which they receive input. Complex cells exist in layers II, III, V, and VI. Fibres projecting from different layers of the PVC have different destiations; for example, the complex cells in layer VI project mainly back to the LGN.



POSITIONS OF RECEPTIVE FIELDS (*numbered from 1 to 9*) of cortical neurons mapped by an electrode penetrating at roughly a right angle to the surface are essentially the same (*left*), although the fields are different sizes and there is some scatter. In an oblique penetration (*right*) from two to four cells were recorded, at .1-millimeter intervals, at each of four sites (*numbered from 1 to 4*) one millimeter apart. Each group includes various sizes and some scatter, but now there is also a systematic drift: fields of each successive group of cells are somewhat displaced.

A particular cell in the PVC has the same orientation-specificity, receptive field position, and ocular dominance patterns as those directly above or below it. That is, an electrode penetrating at roughly 90° to the surface of the PVC registers the same or similar orientational and ocular preference and receptive field position in cells from all layers. Conversely, in an oblique penetration of the cortex, receptive field position and orientation shift slightly from layer to layer, whereas ocular preference alternates regularly.



GROUPING OF CELLS according to ocular dominance was revealed by physiological studies. In one typical vertical penetration of the cortex (*1*) a microelectrode encounters only cells that respond preferentially to the left eye (L_i) and, in layer IV, cells that respond only to the left eye (*L*); in another vertical penetration (*2*) the cells all have right-eye dominance (R_i) or, in layer IV, are driven exclusively by the right eye (*R*). In an oblique penetration (*3*) there is a regular alternation of dominance by one eye or the other eye. Repeated penetrations suggest that the cortex is subdivided into regions with a cross-sectional width of about .4 millimeter and with walls perpendicular to the cortical surface and layers: the ocular-dominance columns.