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, as you may remember from Chapter 1, is the receptive field of the ganglion cell, the region of retina over which we can influence the ganglion cell’s firing by light stimulation.

This general plan holds for the entire retina, but the details of connections vary markedly between the fovea, which corresponds to exactly where we are looking—our center of gaze, where our ability to make out fine detail is highest—and the far outer reaches, or periphery, where vision becomes relatively crude. Between fovea and periphery, the direct part of the path from receptor to ganglion cell changes dramatically. In and near the fovea, the rule for the direct path is that a single cone feeds a single bipolar cell, and a single bipolar in turn feeds into one ganglion cell. As we go progressively farther out, however, 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.

The general scheme of the retinal path, with its direct and indirect components, was known for many years and its correlation with visual acuity long recognized before anyone understood the significance of the indirect path. An understanding suddenly became possible when the physiology of ganglion cells began to be studied.

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**THE RECEPTIVE FIELDS OF RETINAL GANGLION CELLS:**

**THE OUTPUT OF THE EYE**

In studying the retina we are confronted with two main problems: First, how do the rods and cones translate the light they receive into electrical, and then chemical, signals? Second, how do the subsequent cells in the next two layers—the bipolar, horizontal, amacrine, and ganglion cells—interpret this information? Before discussing the physiology of the receptors and intermediate cells, I want to jump ahead to describe the output of the retina—represented by the activity of the ganglion cells. 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. Understanding it can help us to understand why the cells in the intermediate stages are wired up as they are, and will help explain the purpose of the direct and indirect paths. If we know what ganglion cells are telling the brain, we will have gone far toward understanding the entire retina.
Two neighboring retinal ganglion cells receive input over the direct path from two overlapping groups of receptors. The areas of retina occupied by these receptors make up their receptive-field centers, shown face on by the large overlapping circles.

You can see why by glancing at the simplified circuit in the diagram above: the cell colored purple and the one colored blue receive inputs from the overlapping regions, shown in cross section, of the appropriate colors. Because of divergence, in which 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.

**DIMENSIONS OF RECEPTIVE FIELDS**

My third comment is an attempt to relate these events in the retina to everyday vision in the outside world. 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. The finer the detail conveyed by each of these fibers, the crisper will be our image of the world.
The more of a given region, on or off, the stimulus filled, the greater was the response, so that maximal on responses were obtained to just the right size circular spot, and maximal off responses to a ring of just the right dimensions (inner and outer diameters). Typical recordings of responses to such stimuli are shown on this page. The center and surround regions interacted in an antagonistic way: the effect of a spot in the center was diminished by shining a second spot in the surround—as if you were telling the cell to fire faster and slower at the same time. The most impressive demonstration of this interaction between center and surround occurred when a large spot covered the entire receptive field of the ganglion cell. This evoked a response that was much weaker than the response to a spot just filling the center; indeed, for some cells the effects of stimulating the two regions cancelled each other completely.

An off-center cell had just the opposite behavior. Its receptive field consisted of a small center from which off responses were obtained, and a surround that gave on responses. The two kinds of cells were intermixed and seemed 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 probably 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, as you can see from the graph on the next page. With a spot covering the entire field, the center either just barely wins out over the surround, or the result is a draw. This effect explains why neurophysiologists

Left: Four recordings from a typical on-center retinal ganglion cell. Each record is a single sweep of the oscilloscope, whose duration is 2.5 seconds. For a sweep this slow, the rising and falling phases of the impulse coalesce so that each spike appears as a vertical line. To the left the stimuli are shown. In the resting state at the top, there is no stimulus; firing is slow and more or less random. The lower three records show responses to a small (optimum size) spot, a large spot covering the receptive-field center and surround, and a ring covering the surround only. Right: Responses of an off-center retinal ganglion cell to the same set of stimuli shown at the left.
The two main types of retinal-ganglion-cell receptive fields are on center, with inhibitory surround, and off center, with excitatory surround. "+" stands for regions giving on responses, "-" for regions giving off responses.

Before Kuffler had such lack of success: they had recorded from these cells but had generally used diffuse light—clearly far from the ideal stimulus.

You can imagine what a surprise it must have been to observe that shining a flashlight directly into the eye of an animal evoked such feeble responses or no response at all. Illuminating all the receptors, as a flashlight surely does, might have been expected to be the most effective stimulus, not the least. The mistake is to forget how important inhibitory synapses are in the nervous system. With nothing more than a wiring diagram such as the one on page 27, we cannot begin to predict the effects of a given stimulus on any given cell if we do not know which synapses are excitatory and which are inhibitory. In the early 1950s, when Kuffler was recording from ganglion cells, the importance of inhibition in the nervous system was just beginning to be realized.

Before I go on to describe the receptors and other retinal cells, I want to make three additional comments about receptive fields. The first is a general comment about receptive fields as a concept; the other two comments are specifically about the receptive fields of retinal ganglion cells: their overlap and their dimensions.

**THE CONCEPT OF A RECEPTIVE FIELD**

Narrowly defined, the term *receptive field* refers simply to the specific receptors that feed into a given cell in the nervous system, with one or more synapses intervening. In this narrower sense, and for vision, it thus refers simply to a region on the retina, but since Kuffler’s time and because of his work the term has gradually come to be used in a far broader way. Retinal
had a substructure: stimulating different parts of the receptive fields gave qualitatively different responses, and stimulating a large area resulted in cancellation of the effects of the subdivisions rather than addition. As presently used, receptive field tends to include a description of the substructure, or if you prefer, an account of how you have to stimulate an area to make the cell respond. When we speak of “mapping out a cell’s receptive field”, we often mean not simply demarcating its boundaries on the retina or the screen the animal is looking at, but also describing the substructure. As we get deeper into the central nervous system, where receptive fields tend to become more and more complex, we will find that their descriptions become increasingly elaborate.

Receptive-field maps are especially useful because they allow us to predict the behavior of a cell. In the case of retinal ganglion cells, for example, suppose we stimulate an on-center cell with a long, narrow rectangle of light, just wide enough to span the receptive-field center, and long enough to go beyond the whole field, center plus surround. We would predict from the on-center map on page 42 that such a stimulus would evoke a strong response, since it covers all the center and only a small fraction of the antagonistic surround. Furthermore, from the radial symmetry of the map we can predict that the magnitude of the cell’s response will be independent of the slit’s orientation. Both predictions are confirmed experimentally.

THE OVERLAP OF RECEPTIVE FIELDS

My second comment concerns the important question of what a population of cells, such as the output cells of the retina, are doing in response to light. To understand what ganglion cells, or any other cells in a sensory system are doing, we have to go at the problem in two ways. By mapping the receptive field, we ask how we need to stimulate to make one cell respond. But we also want to know how some particular retinal stimulus affects the entire population of ganglion cells. To answer the second question we need to begin by asking what two neighboring ganglion cells, sitting side by side in the retina, have in common.

The description I have given so far of ganglion-cell receptive fields could mislead you into thinking of them as forming a mosaic of nonoverlapping little circles on the retina, like the tiles on a bathroom floor. Neighboring retinal ganglion cells in fact receive their inputs from richly overlapping and usually only slightly different arrays of receptors, as shown in the diagram on this page. This is the equivalent of saying that the receptive fields almost completely overlap.
Two neighboring retinal ganglion cells receive input over the direct path from two overlapping groups of receptors. The areas of retina occupied by these receptors make up their receptive-field centers, shown face on by the large overlapping circles.

You can see why by glancing at the simplified circuit in the diagram above: the cell colored purple and the one colored blue receive inputs from the overlapping regions, shown in cross section, of the appropriate colors. Because of divergence, in which 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.

**DIMENSIONS OF RECEPTIVE FIELDS**

My third comment is an attempt to relate these events in the retina to everyday vision in the outside world. 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. The finer the detail conveyed by each of these fibers, the crisper will be our image of the world.
This 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. The more straightforward description is simply its size on the retina. This has the disadvantage of being not very meaningful in the everyday scale of things. Alternatively, you could measure receptive-field size in the outside world, for example, by taking its diameter on a screen that an animal faces, but you would then have to specify how far the screen is from the animal’s eyes. The way around this problem is to express receptive-field size as the angle subtended by the receptive field on the screen, at the animal’s eye, as shown in the figure on this page. We calculate this angle in radians simply by dividing the field diameter by the screen distance, but I will use degrees: \((\text{radians} \times 180)/\pi\). One millimeter on the human retina corresponds to an angle of about 3.5 degrees. At 54 inches screen distance, 1 inch 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.

Receptive fields differ in size from one ganglion cell to the next. In particular, the centers of the receptive fields vary markedly and systematically in size: they are smallest in the fovea, the central part of the retina, where our visual acuity—our ability to distinguish small objects—is greatest; they get progressively larger the farther out we go, and meanwhile our acuity falls off progressively.

In a monkey the smallest field centers yet measured subtend about 2 minutes of arc, or about 10 micrometers (0.01 millimeters) on the retina. These ganglion cells are in or very close to the fovea. 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 500 feet.
Far out in the periphery of the retina, receptive-field centers are made up of thousands of receptors and can have diameters of 1 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. These three trends are clues that help us understand the meaning of the direct and indirect paths from receptors to ganglion cells. The strong implication is that the center of the receptive field is determined by the direct path and the antagonistic surround by the indirect one, and that the direct path sets limits on our acuity. To obtain more evidence for this conclusion, it was necessary to record from the other cells in the retina, as I will describe in the next section.

THE PHOTORECEPTORS

It was many years before much progress was made in the physiology of the receptors, bipolars, horizontal cells, or amacrine cells. There are many reasons for this: vascular pulsations bedevil our attempts to keep microelectrodes in or close to single cells; receptors, bipolars, and horizontal cells do not fire impulses, so that recording the much smaller graded potentials requires intracellular techniques; and it is hard to be certain which of the cell types our electrode is in or near. We can circumvent some of these problems by choosing just the right animal: retinas of cold-blooded vertebrates survive when taken out of the eye and bathed in oxygenated salt water, and eliminating the blood circulation eliminates arterial pulsations; the mudpuppy (a kind of large salamander) has very large cells, easy to record from; fish, frogs, turtles, rabbits, and cats all have special advantages for one or another kind of study, so that many species have been used in the study of retinal physiology. The problem with using so many species is that the details of the organization of the retinas can differ markedly from one species to the next. Moreover, our knowledge of the primate retina, one of the most difficult to record from, has until recently had to depend largely on inferences from the results pooled from these other species. But progress in primates is accelerating as the technical difficulties are overcome.

In the past few years, our understanding of the way in which a rod or cone responds to light has dramatically increased, so much so that one has the feeling of at last beginning to understand how they work.

Rods and cones differ in a number of ways. The most important difference is in their relative sensitivity: rods are sensitive to very dim light, cones require