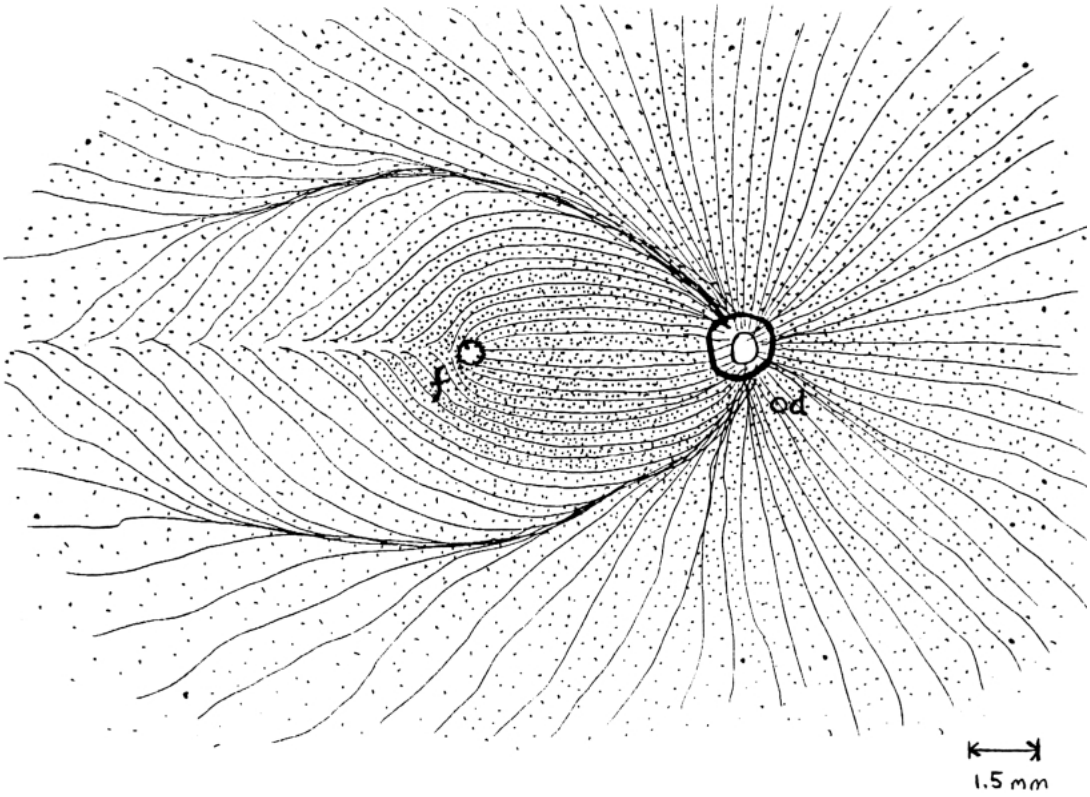

Figure 2-5: Distribution of retinal ganglion cell bodies (small dots) and axons (thin lines) in the human retina. Drawing by Dr. Joe Rizzo. Abbreviations: *f* - fovea; *od* - optic disk.

originating at all portions of the retina converge to form the optic nerve (Figure 2-5). Nasal to the disk (left side of Figure 2-1, right side of Figure 2-5), axons form straight line paths. Temporal to the disk (the opposite side), axons not originating in the fovea form arched paths around it. The *fovea* is a round region located on the left side of the optic disk as drawn in Figure 2-5. In cross-section, the fovea is a pit-shaped depression on the inner surface of the retina. The foveal depression is characterized by decrease in thickness of the inner layers (5-9) and an increase thickness of the photoreceptor layers (2-4). Cone densities are highest within the fovea, with a minimum center to center spacing of two to three microns. Presumably, the inner layers in this region are thinned in order facilitate light transmission to the foveal cones. The retina is thickest at the outer margin of the fovea, where ganglion cells are stacked as many as seven or eight layers deep. The high cell density and specialized connections (see section 2.1.3) of the fovea account for the fact that the portion of the visual field which projects onto this region can be seen with greatest spatial resolution. The fovea is part of a larger region of the retina known as the *macula*. Neurons in the macula are smaller and more uniform in size than elsewhere, and are present at higher densities. Ganglion cells within this area, for example, are stacked at least two layers deep. The remaining regions outside of the macula are called the *peripheral retina*.

Cell densities decrease and cell sizes increase at increasing distances from the central

area[5]. While there is a loss in visual acuity corresponding to the lower cell density in more peripheral regions, physiological recordings from central and peripheral cells suggest that the same basic functional classes of cells exist throughout the retina. In the central retina, a small number of cells will converge upon a ganglion cell of a given type through its small dendritic field. In the peripheral retina, by contrast, a larger number of cells converge upon a ganglion cell of the same type through its large dendritic field.

2.1.3 Information processing in the retina

In the preceding description of retinal neurons, certain types of cells were subdivided according to their responses to small spots of light. This criterion distinguished, for example, the On-center ganglion cells from the Off-center cells. The fact that a given cell will respond preferentially to certain stimuli leads us to regard it as an information processing element, and by extension to think of the retina as an information processing system.

The input to this system is a spatial and temporal pattern of light entering the eye from the visual field. The output is a collection of ganglion cell responses, each a temporal pattern of action potentials conducted away from the retina by a single axon. Between input and output, as we have seen, is an alternating series of cellular and synaptic layers. Signal flow through these layers might be described in terms of *vertical* and *lateral* components. A signal propagating in the pure vertical direction traverses the cellular layers, from photoreceptors to bipolar cells to ganglion cells. A signal traveling in the pure lateral direction, on the other hand, propagates within a single cellular layer, either through networks of horizontal or amacrine cells. This section will focus both on observed characteristics of such input/output relationships and also on their related signal pathways within the retina.

Receptive fields and spatial sampling

While efforts are currently being made to record activity from several cells simultaneously [34], most studies of retinal input/output behavior have concentrated on individual cells. The basic experiments performed in these studies consisted of presenting various light stimuli to the retina while monitoring the behavior of a single cell with a recording electrode. These experiments revealed that light must fall on the retina within a restricted area, referred to as the *receptive field*, in order to influence a cell's behavior. Ganglion cell receptive fields in the cat retina were found to vary between 0.8mm and 2mm in diameter for centrally located cells[31]. In general, receptive fields become progressively larger with increasing eccentricity [49].

Because its receptive field is restricted, each ganglion cell is concerned with light emanating from the restricted area within the visual scene. Thus a spatial decomposition takes place in the retina whereby the visual field is parceled according to ganglion cell receptive fields. Receptive fields of adjacent ganglion cells may overlap, however, so that light impinging on any one region of the retina will produce output from many different ganglion cells.

Spatial sampling in ganglion cells originates at the photoreceptors. To a first approximation, the size of a photoreceptor's receptive field will be determined by the diameter of

[5] An exception to this rule are the rods, which are absent in the central fovea and whose density increases with retinal eccentricity.

its outer segment[6]. Though photoreceptors and ganglion cells are alike in that both possess receptive fields, it would be an oversimplification to assume a one-to-one correspondence between those of the photoreceptors those of the ganglion cells. In general, signals from many photoreceptors will converge on a single ganglion cell through a combination of vertical and lateral pathways.

The On and Off channels

On-center and Off-center ganglion cells were described briefly in section 2.1.1. Two important characteristics of On-center and Off-center responses are illustrated in Figure 2-6. First, the cells respond to both *temporal* and *spatial* variations in illumination. Temporal response properties are revealed by the middle trace of the Figure ("Center and surround illumination"), where illumination of the receptive field is spatially uniform: On-center cells are excited by temporal increases in illumination and inhibited by decreases, whereas Off-center cells are excited by temporal decreases in illumination and inhibited by increases. The top and bottom traces of the Figure ("Center stimulation" and "Surround stimulation", respectively) reveal spatial response properties: when more light falls on the receptive field center than on the surround, On-center cells respond vigorously and Off-center cells are inhibited; when less light falls on the center than on the surround, the responses are reversed. It should also be noted that certain types of cell responses are generated by both the spatial and temporal pattern of a stimulus. For example, On-center Y cells (see below) are maximally excited at the onset of center stimulation (not shown in the Figure). The second important characteristic is the antagonistic, center/surround receptive field organization exhibited by On-center and Off-center cells. As revealed in Figure 2-6, both excitatory and inhibitory effects are most pronounced when illumination is restricted to either the receptive field center (top trace) or the surround (bottom trace).

Both the On/Off dichotomy and the antagonistic center/surround receptive field organization arise at the level of bipolar cells. The receptive field organization, as discussed in section 2.1.1, is thought to stem from opposing influences produced in the bipolar cell by photoreceptors and horizontal cells. Direct interactions between photoreceptors and bipolar cells produce a center response, while the surround response is mediated by horizontal cells. As for the On/Off dichotomy, recall that On-center and Off-center cone bipolar cells are distinguished by the polarity of potential they produce in response to illumination of the retina. On-center cells depolarize to illumination of their receptive field centers, while Off-center cells hyperpolarize. By contrast, photoreceptors and horizontal cells only hyperpolarize.

It is initially mysterious in light of these facts that cone bipolar and ganglion cells produce both hyperpolarizing and depolarizing potentials. The single polarity to double polarity conversion which takes place in the retina is due in part to two mechanisms. First, it has a pharmacological basis: though photoreceptors are believed to use a single type of neurotransmitter [54], the On-center and Off-center bipolars differ in the type of neurotransmitter receptor found in their dendritic membranes [62]. Second, anatomical evidence suggests that the conversion may be carried out within the rod pathway as well. While rod bipolar cells are thought to only produce depolarizations, these cells terminate mostly on the AII type amacrine cell. AII amacrine cells make inhibitory or hyperpolarizing synapses onto Off-center cone bipolar and ganglion cells, but make excitatory or depolarizing gap

[6]Lateral interactions between photoreceptors will also contribute a given cell's receptive field, though the role of such interactions in retinal signal flow is not well understood [14].

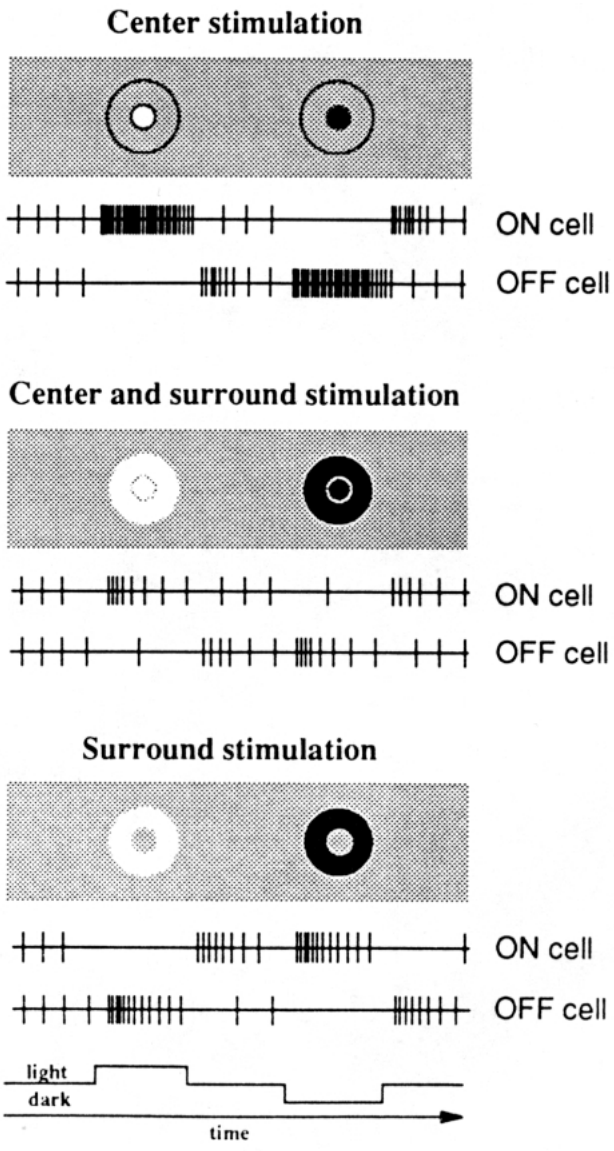

Figure 2-6: Idealized responses of On-center and Off-center ganglion cells. From Schiller [54].