# The fundamental plan of the retina

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**The retina, like many other central nervous system structures, contains a huge diversity of neuronal types. Mammalian retinas contain approximately 55 distinct cell types, each with a different function. The census of cell types is nearing completion, as the development of quantitative methods makes it possible to be reasonably confident that few additional types exist. Although much remains to be learned, the fundamental structural principles are now becoming clear. They give a bottom-up view of the strategies used in the retina's processing of visual information and suggest new questions for physiological experiments and modeling.**

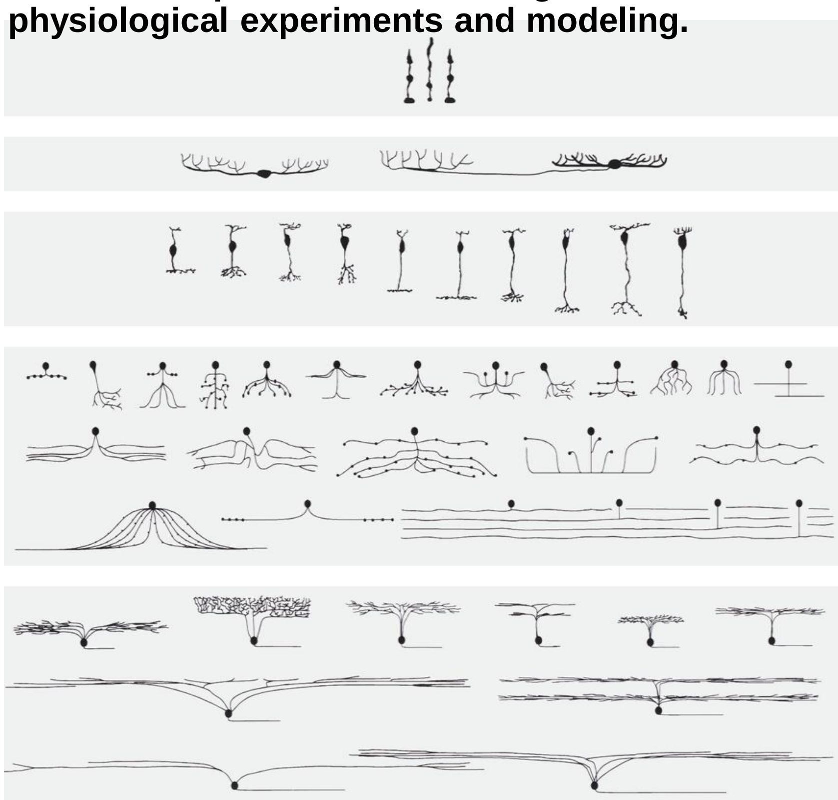

**Fig. 1**. The major cell types of a typical mammalian retina. From the top row to the bottom, photoreceptors, horizontal cells, bipolar cells, amacrine cells and ganglion cells. Amacrine cells, the most diverse class, have been studied most systematically in the rabbit3,4, and the illustration is based primarily on work in the rabbit. Most of the cells are also seen in a variety of mammalian species. The bipolar cells are from work in the rat39; similar ones have been observed in the rabbit, cat16 and monkey17. For steric reasons, only a subset of the wide-field amacrine cells is shown.

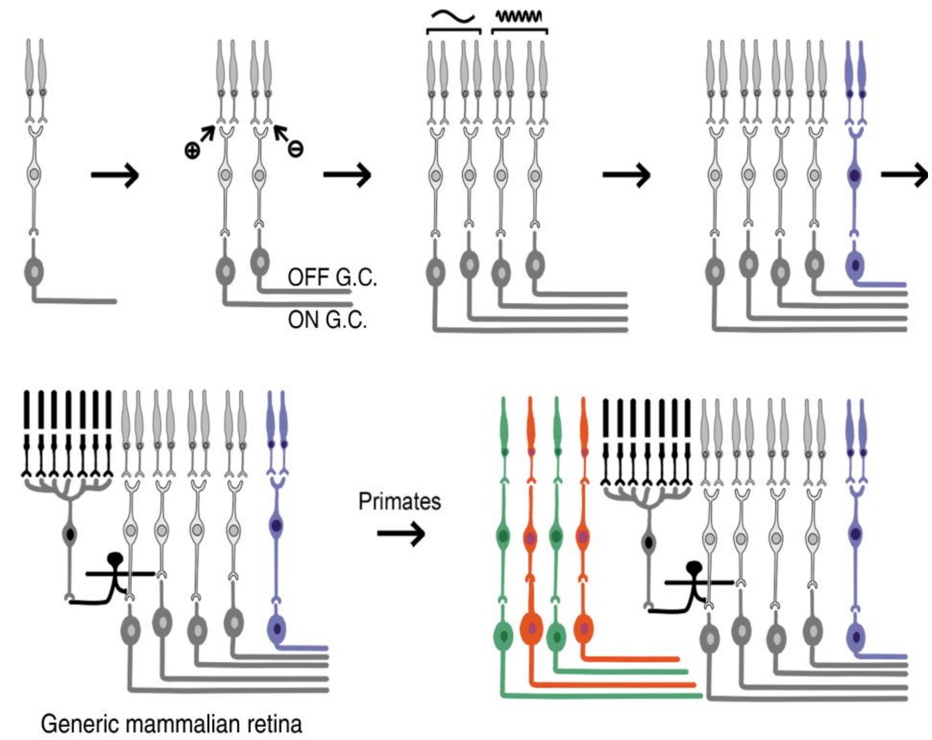


**Fig. 2.** The bipolar cell pathways of mammalian retinas, assembled from individual components. This diagram is intended to emphasize the overall organization of the parallel channels, and much detail is omitted. Many primate retinas have midget bipolar and ganglion cells, but only a few have a separate red and green channels. Rods are not as clumped as would be suggested here. For visual clarity, cones are shown contacting only a single bipolar cell each; in fact, all cones contact several bipolar cells, as shown in Figs. 3, 4 and 6. For the detailed synaptology of the rod pathway, see refs. 36, 37, 125.

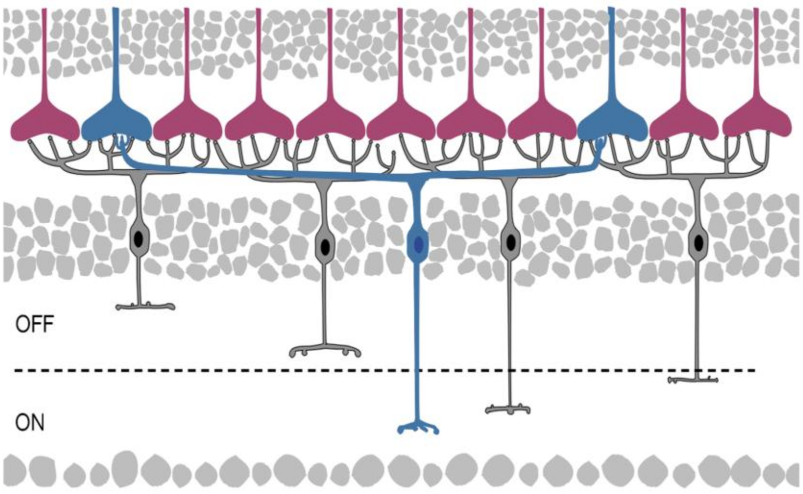


**Fig. 3.** The connections with cones and axonal stratification of different types of bipolar cells. Five different types of bipolar cells are illustrated. Two of them are diffuse (chromatically nonselective) ON bipolar cells terminating in the inner half of the inner plexiform layer. Two are diffuse OFF bipolar cells terminating in the outer half. Each samples indiscriminately from the spectral classes of cones. The blue cone bipolar, however, contacts only blue cones and thus is spectrally tuned to short wave lengths. Within the ON or OFF sublayer, axons of the bipolar cells terminate at different levels, indicating that they contact different sets of postsynaptic partners. After refs. 9 and 17.

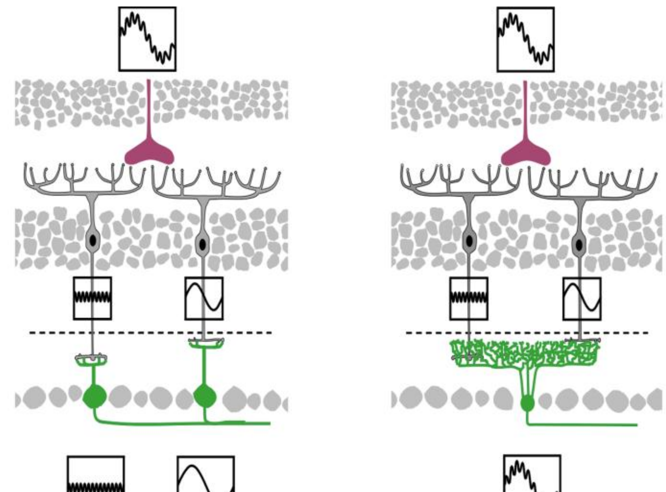

**Fig. 4.** How transient (high-pass) and sustained(low-pass) bipolar cells decompose the output of a cone. The resulting high- and low-frequency channels can contact narrowly stratified ganglion cells (a), in which case the two frequency bands are transmitted via separate, parallel channels to the brain. Bottom, a more broadly stratified ganglion cell (such as a beta cell) receives input from both types of bipolar cells123. Such a ganglion cell(b) has a broadband response. Many such combinations are possible, as are many permutations of input from amacrine cells.

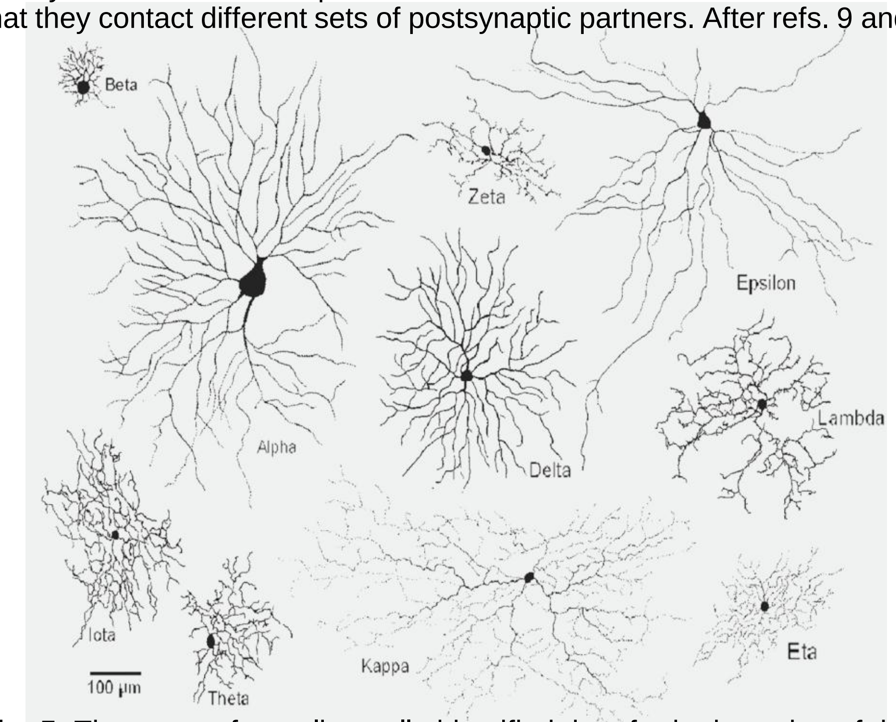


**Fig. 5**. The types of ganglion cells identified thus far in the retina of the cat. Ongoing work in the rabbit and monkey confirms this diversity, and many of the cells observed are probably homo logs of those seen in the cat. Courtesy of D. Berson77–80.

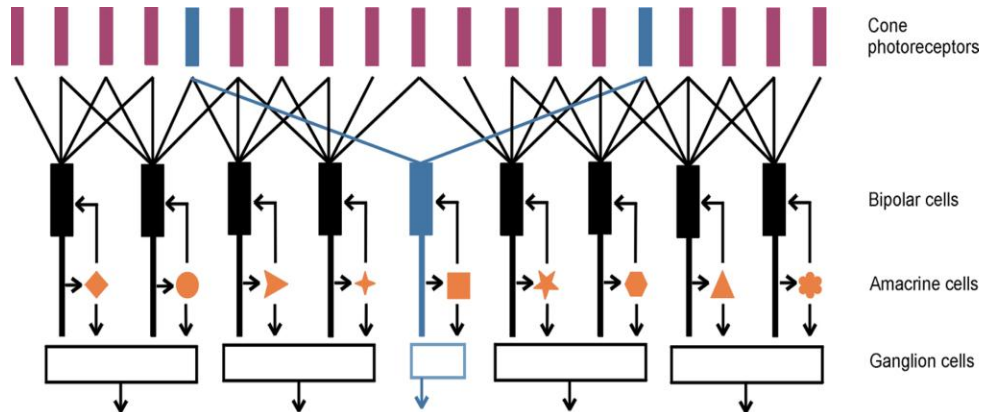


**Fig. 6**. The fundamental signal-carrying pathways of a generic mammalian retina, reduced to a conceptual minimum. Each type of bipolar cell (black)transmits a different type of information to the inner retina. The information that it transmits is determined by the bandwidth of the cones that it contacts, the number and type of those cones, the transfer function of the cone to bipolar synapse, and its interplay with amacrine cells. This is a minimal representation of the amacrine cells, which also include wide-field cells and which have synaptic contacts among each other. The different types of bipolar cells are contacted by distinct types of amacrine cells, in a variety of synaptic arrangements. These converge upon the retinal ganglion cells, in which specific combinations of bipolar and amacrine inputs create many functional types of ganglion cells.