On the Understanding of Retinal Topography
A "Two-Axis" Model of Mammalian Retina

9.1. The Problem: The Variability of Retinal Topography
A remarkable feature of mammalian retina is the constancy of its organization across its thickness. In the retinas of all mammals, three layers of nerve cells are recognized, separated by plexiform (synaptic) layers. The receptor cells lie on the outer surface of the retina, with the tips of their outer segments enclosed by cells of the pigment epithelium; bipolar, amacrine, interplexiform, and horizontal cells form the middle layer, and ganglion cells and their axons form the innermost layers of the retina.

By contrast, there is considerable diversity among mammalian species in the structure of the retina along its other two axes, viz., its width and height. The variation is particularly well documented in the ganglion cell layer, in which a fovea may be present or absent, a visual streak may be a dominant feature or barely detectable, and the populations of ganglion cells that project to different sides of the brain may vary widely in their relative numbers, and in the degree to which they are spatially segregated. Moreover, recent studies have provided evidence of long-unsuspected differences in the properties of ganglion cells between areas of the retina nasal and temporal to the area centralis or fovea, and between the visual streak and other regions of peripheral retina. It has been suggested that these latter differences are related to the different functional roles and phylogenetic histories of these different areas of the retina. Regional variations have also been described in other layers of the retina, adding to the range of variation requiring explanation.

In this chapter, I attempt to provide a conceptual framework or "model" within...
which this variation in retinal topography can better be understood. The model relies on a variety of observations, but particularly on patterns of retinal distribution and nasotemporal division of the different classes of ganglion cells that have been described in various mammals. In brief summary, it is argued (1) that a basic pattern of retinal topography can be discerned that is common to a wide range of mammals and (2) that the considerable variation in topography between mammalian species can be fruitfully regarded as adaptations of that basic pattern. The model is, however, restricted to mammalian retina. In many fish, amphibians, and reptiles, retinal cells proliferate constantly throughout life in a zone at the edge of the retina (whereas in mammals the proliferation ceases in fetal life or infancy), and the effect of this steady proliferation on retinal topography has still to be described. In birds, the development in many species of two separate foveas in each retina, and the absence of any retinal projection to the ipsilateral side of the brain, suggest a quite separate line of development of retinal topography. Much needs to be learnt of retinal topography and ganglion cell groupings in nonmammalian vertebrates (and no doubt in mammals as well) before a model of retinal topography applicable to all vertebrates can be attempted. Nevertheless, the model suggested here has (I would argue) two principal useful features:

1. It provides a single framework for understanding the variety of retinal topography found among mammals, and relating it to their phylogenetic history and visual behavior.

2. It makes substantive generalizations and predictions about major features of retinal topography, whose testing should both assess the model and advance understanding of retinal organization.

9.2. A TWO-AXIS MODEL OF THE TOPOGRAPHY OF MAMMALIAN RETINA

The model is represented diagrammatically in Fig. 9.1, and the legend to that figure describes some of its detail. Its major premises and postulates are:

1. The topography of mammalian retina can be usefully regarded as organized around two axes, the approximately horizontal axis of the visual streak, and the approximately vertical axis of nasotemporal division. The former axis follows the length of the visual streak; this is an elongated region of specialized retinal structure that extends across much of the width of the retina. The latter axis runs approximately vertically across the zone of transition between the nasal region of the retina, from which ganglion cells project to the contralateral hemisphere of the brain, and the temporal region of the retina, to which ipsilaterally projecting ganglion cells are restricted.

2. The visual streak and the nasotemporal division of the retina represent different aspects of its function and phylogenetic development. The streak specialization seems appropriate to allow the animal to scan large parts of its visual field without eye movements; while the different laterality of projection of nasal and temporal areas of the retina seems related to the function of frontalized, binocular vision.