Excerpts from

PROCESSES IN ANIMAL VISION:

including,

ELECTROCHEMISTRY OF THE NEURON

This material is excerpted from the full β-version of the text. The final printed version will be more concise due to further editing and economical constraints. A Table of Contents is at the end of this paper.

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Part A
Environment and Physiology of Vision

"I am never content until I have constructed a mechanical model of the subject I am studying. If I succeed in making one, I understand; otherwise I do not." Lord Kelvin

In developing a complete understanding of the visual processes in animals, documenting the physical environment surrounding the processes is important. Documenting the technology available to contribute to this understanding is equally important before going into the detailed analyses. Whereas the physical environment related to vision has generally been static with time, except the availability of new technology such as the laser as a light source, the technology environment available to the researcher has continued to race ahead throughout the 20th century. This has been especially true of the last 50 years. Because of these changes, reviewing the impact of this technology is appropriate before proceeding.

PART A develops the common architecture of all animal vision and demonstrates the potential for tetrachromatic vision in a plurality of animals. The large terrestrial animals and most arthropods are limited to different trichromatic subsets of the tetrachromatic spectra by evolution.

This PART is subdivided into four chapters.

Chapter 1, Introduction, is designed to describe the perspective and focus of this work in sufficient detail to form a roadmap for the reader. It includes; an initial discussion of terminology related to vision, a series of simple experiments designed to familiarize the reader with several concepts related to vision, a discussion of the modeling of biological systems, and the need for much more careful experiment design and execution than used in the past. It also includes basic block diagrams attempting to illustrate the visual systems of different animals and their place in the evolutionary process as a result of their adaptation to various environmental niches.

This discussion results in a proposed new phylogenic tree based on the apparent evolution of the visual process. It is shown that this tree is also compatible with the occurrence of Vitamin A_1 and Vitamin A_2 in different animal species (occasionally as a function of time). This tree suggests that all animals share a common ancestor, an early bilateral worm contemporary with if not actually *Planaria*. It will be shown later that this common ancestry does not support a fundamental difference in the operation of the vertebrate and non-vertebrate eye as suggested in some literature.

A more extensive, but still elementary discussion follows describing the various generic subsystems of the visual system. In some cases, these systems are seen to vary systematically by phylum and sometimes within a phylum. The chapter concludes with a summary of the findings of this work and the presentation of some new descriptors of visual performance suggested by this work.

Two areas related to vision are particularly deserving of significant review before proceeding and are included in this Chapter. Both the levels of understanding of the principals of optics and the fundamental operating principal of the eye displayed in the biological literature are perplexing. The biological literature appears to rely on the use of optical principals grouped under the honorary designation of Gaussian Optics. It does this without recognizing that the underlying technical designation is paraxial optics, i.e., *an elementary method of optical analysis limited to light rays found very near and parallel to the optical axis*. Such paraxial optics is hardly adequate for the proper understanding of the operation of the eye. Similarly, the literature since the middle 1800's has treated the retina as a kind of photographic film, i.e., a device that integrates the illumination level over a fixed period of time and creates a signal proportional to that integral on a point by point basis over the surface of the retina. It has done this in the face of overwhelming evidence that the individual photodetectors of the eye, and the retina as a whole, are not able to generate such a signal. The photodetectors are only able to generate a signal proportional to the short term change in illumination. This fact that the fundamental eye operates as a change detector and is blind to a fixed image illuminated by a constant source of illumination must be appreciated if the overall operation of the eye is to be understood. Section 2.3 will review the principals and laws of optics applicable to the eye in greater detail than in this introduction. PART E will examine the fundamental operating mode of the eye and how that mode is adapted to alternate levels of performance on a species by species basis.

Chapter 2, Environment, Coordinate Reference System and First Order Operation, is designed to begin the substantial task of defining the framework required to understand the visual process in detail and to avoid simplistic conclusion based on the use of partial or "floating models." The use of inadequate models in the past has caused great and unjustifiable confusion within the vision research community. This confusion has carried over into and propagated throughout the general literature of biology. The physical environment, particularly the radiation environment, is explored in some detail. The development of an adequate coordinate system is also stressed. The bulk of the chapter is concerned with the details of the physical optical system of the eye, particularly the human eye. Several features are discussed that are not available in the general literature, particularly the inadequacy of Gaussian Optics for research in vision. Because of its critical role in human vision, the oculomotor system is reviewed. The Chapter closes with a brief introduction to the signaling paths of vision with emphasis on the signaling exiting the retina.

Chapter 3, Description of the Retina, introduces the body of the work with a major section on terminology. The retina is explored from both the morphological and functional perspective. The morphological perspective is reviewed with respect to both topography and histology. It is at the latter level that both the mosaic characteristics and the individual laminates of the retina can best be explored. Especially important is the description of the orientation of the photoreceptors showing that they always point toward the aperture of the optical system and are not generally perpendicular to the surface of the retina. The seldom studied vascular system of the retina is explored in detail because of its little known but major role in the adaptation properties of vision. A first level block diagram of the signaling system associated with the retina is developed.

Chapter 4, The Photoreceptor Cell of the Chordate Eye, provides both an overview and a detailed description of the photoreceptor cell. It begins with a section on additional terminology and initially discusses the histology of photoreceptor cells as found in the animal kingdom. With the chordate photoreceptor cell in proper context within the animal kingdom, this unique neural cell is discussed in considerable detail. The histological fact that the cell is a **neuro-secretory cell**, in common with the general class of neurons, is stressed. Although virtually never mentioned in the literature, this fact is critical to the understanding of the operation of the cell. It is this neuro-sectretory character that supports the proposition of this work that the so-called **Outer Segment of the photoreceptor cell is an external component associated with but not an integral part of the cell**. The fact is stressed that, contrary to a series of widely published caricatures of the early 1970's, the **Outer Segment is not enclosed by a cellular membrane**. The functions of the photoreceptor cell are not well understood in the literature. To improve this situation, the photoreceptor cell is shown in exploded view to consist of three primary sections. The growth and metabolism portion is focused on the maintenance of the cell and both the secretion of the protein opsin and its formation into disks. These disks form the structure of the Outer Segment, a space-frame like structure optimized for its role in the photodetection process.

The Outer Segment is the second section of the photoreceptor, and arguably the most unique component of the system. This component, when complete, is very dynamic. The individual disks, following formation, exist for approximately 12 weeks in the human eye before being phagocytized by the cells of the Retinal Pigment Epithelium (RPE). This process is caused by the continual formation of new disks within the cup formed at the end of the Inner Segment of the photoreceptor cell. These new disks continually push earlier disks out of the cup and toward the RPE. Following formation, the individual opsin based disks are coated with the chromophores of vision that are secreted from the RPE cells. The resulting coated disks are now sensitive to light. They are particularly sensitive to light arriving perpendicular to the surface of each disk because of the unique liquid crystalline structure of the chromophore coating.

The coated disks of the Outer Segment are uniquely suited to the efficient interception of visual radiation due to the unique chemical nature of the coatings which is discussed in **Chapter 5**. The chromophore coating exhibits a very large absorption cross-section to visual radiation and efficiently coverts the energy of the photons into the energy of an excited molecule. However, their chemical structure prevents the dissipation of the resultant energy through re-radiation or thermal means. The energy absorbed by the disks is transferred to the third, neural portion of the photoreceptor cell through a highly specialized process. This process has not been reported previously in the biological literature. It leads to the creation of the electrical signal that is transported through the rest of the visual system in order to support the overall visual function. The interface between the disks of the Outer Segment and the neural portion of the photoreceptor cell employs an active electrolytic semiconductor device, named an Activa in a truly spectacularly efficient circuit that is discussed in detail in **Chapter 12.**

The neural role of the photoreceptor cell has not previously been detailed in the literature. It begins with its dendritic structure that emanates from the ciliary collar and extends along the side of the Outer Segment. This structure has usually been described as cilia made up of microtubules. However, these cilia are in fact dendritic structures. The detailed description of the signal path through the photoreceptor cell to its termination at the pedicel of the cell is also detailed in **Chapter 12**.

Chapter 4 closes with a discussion of the functional (electrical) performance of the neural portion of the photoreceptor cell. It defines the uniquely passive electrical performance of the Outer Segment, and both the quiescent and dynamic operation of the cell characterized by the electrical potentials of its axon as measured at it's pedicel. The adaptation amplifier is defined as an integral part of the photoreceptor cell. For the first time, the role of the vascular system, in providing electrical power to the neural system, is presented. The glutamates play a crucial role in the electrical operation of the neural system through a process known as electrostenolytics. There is also a discussion of the signal recording techniques used in clinical evaluation of the eye.