The Biological Vision System:
Introduction; Environment & Review of Eyes in Different Species

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https://neuronresearch.net/vision/

Abstract: Chapter 1 of "Processes in Biological Vision" begins by reviewing some fundamental groundwork supporting this extensive work. It then presents an overview of the total work. **Section 1.2** develops the recent impact of DNA research on the phylogeny of man, Homo sapien. That activity is suggesting that the term anthropoids may be singular and that the human is fundamentally distinct from the primates. **Sections 1.3** & **1.4** review a great many processes and mechanisms that will be useful in developing a broader understanding of the visual modality than proviously achieved. **Section 1.5** establishes a block diagram of the visual modality relevant to all animals and that can be built upon to provide detailed circuit diagrams for individual phylogenic *Orders*. **Section 1.6** provides a broad summary of the performance achieved by human and other animal eyes that are developed in significant detail in later chapters. **Section 1.7.2** reviews the immense breadth of optical systems and retinas employed by animals throughout the animal kingdom. **Section 1.8.1** will introduce the electrolytic neuron at the heart of The Electrolytic Theory of the Neuron. It will provide citations in later Chapters. **Section 1.8.2** extends our knowledge of neural signaling throughout the neural system of all animals as provided by The Electrolytic Theory of the Neuron. **Section 1.9** provides a brief summary of the major findings of this work.

The Chapters are written to stand-alone as much as possible following the block diagram in **Section 1.5**. However, this requires frequent cross-references to other Chapters as the analyses proceed. A Tree of Differences between the complete and contiguous Electrolytic Theory of the Neuron and the earlier and fractured chemical theory of the neuron, is provided in **Section 1.5.2.1**.

While the material in this work is designed for the graduate student undertaking independent study of the vision sensory modality of the biological system, the results can be followed by anyone with a college degree in Science.

Keywords: Biological, Human, Vision, phylogeny, vitamin A, Electrolytic Theory of the Neuron, liquid crystal, Activa, anatomy, histology, cytology

Excerpts from

PROCESSES IN BIOLOGICAL VISION:

including,

ELECTROCHEMISTRY OF THE NEURON

This Chapter is excerpted from the full text. A Table of Contents, List of Figures and an index are at the end of this Chapter.

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Neural Concepts

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October 27, 2019

1 Introduction, Phylogeny & Generic Forms [1]

*"Vision is the **process** of discovering from images what is present in the world, and where it is"* (Marr, 1985)

***When encountering a citation to a Section number in the following material, the first numeric is a chapter number. All cited chapters can be found at https://neuronresearch.net/vision/document.htm ***

1.1 Introduction

While the material in this work is designed for the graduate student undertaking independent study of the vision sensory modality of the biological system, with a certain amount of mathematical sophistication on the part of the reader, the major emphasis is on specific models down to specific circuits used within the neuron.

The Chapters are written to stand-alone as much as possible following the block diagram in **Section 1.5**. However, this requires frequent cross-references to other Chapters as the analyses proceed.

The results can be followed by anyone with a college degree in Science. However, to replicate the (photon) Excitation/De-excitation Equation, a background in differential equations and integration-by-parts is required. Some background in semiconductor physics is necessary to understand how the active element within a neuron operates and the unique character of *liquid-crystalline water* (the backbone of the neural system).

The level of sophistication in the animal vision system is quite remarkable. Until recently, the technology of man was not adequate to provide a proper model and understanding of the overall system, much less a detailed understanding of the system such as that found in humans.

Throughout history, man has only been able to build complex system based on the available knowledge of the day. With this knowledge, man has been able to explain these "man-made" systems to others to the same level as the understanding required to build them. This situation has not existed in the biological systems. Beautifully designed and implemented systems have arisen without depending on the knowledge of man. And man has not been able to explain these natural systems to others because of the lack of understanding required to build them. Because of this situation, man's understanding of biological systems has changed dramatically with the advance of his understanding of technology. It is now time to present a dramatically different explanation of the operation of the visual and neural systems of biology than has previously been available in the literature.

An immense amount of detailed, measured, data is available in the literature, some of it well characterized and controlled, ***much of it is not***!!! Much of this data has appeared in batches resulting from a team with either a charismatic or an industrious leader pursuing a theory or an approach to technical exhaustion. Frequently these teams have veered off the course over time because of the limitations of their theoretical (more often conceptual) model. This can frequently be observed by reading a sequence of papers and observing the entrenching of inadequate theories by later investigators omitting the limitations and caveats placed on the earlier work by the original investigators. Horner[2] has characterized this process clearly. He describes a "*search image*" as a heuristic preconception that the investigator strives to prove. Often, their result shows that they found their exact search image because it agrees with their own prior education. Anything that might have contradicted the image (because it differed from the views of their teacher or their own studies) was overlooked, misinterpreted or dismissed as unimportant.

The pursuit of "*search images*" is clearly demonstrated in the literature of vision. It has frequently been necessary to confirm such "*search images*" in order to gain acceptance in the peer review process. The current wisdom has persisted for the last half of a century and is based on a simple set of such images developed within a chemical construct, largely in spite of the dawn of the electronic age and the subsequent information age. The pursuit of such images has been based on an ionic approach to biochemistry and reliance upon a stereoisomeric hypothesis in the

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[1]Released: October 27, 2019

[2]Horner, J. R. (1997) Dinosaur Lives. NY: Harper Collins pg. 26

absence of creditable alternatives at the time. To a large, extent, this theoretical basis was developed in a technical vacuum. The proposals made within the biochemical community were not correlated with the parallel, and more fully developed, field of photochemistry. Nor did the proposals incorporate many of the tools available within the mathematical and electronics community. Since that time, the field of vision has advanced without incorporating any of the principles of current day semiconductor physics. The result of these parochial actions has been the development of a largely conceptual framework of vision that involves a series of overly complex hypotheses applicable only to small segments of the overall subject. These frameworks of limited scope will be referred to as "floating models" in this work.

Stone[3] provided a remarkable book in 1983 where he attempted to organize the major signaling paths within the visual modality, taking unique care to explain his method of organizing various individual conceptual areas. The book extends far beyond just organizing the labels for retinal ganglion cells. He notes in his Preface,

> "From the initial work [of classifying only ganglion neurons] there emerged a new understanding of these centers, leading to the idea of "parallel processing" in the visual system. . . . As a consequence, only the first of the three parts of this monograph is concerned with the classification of retinal ganglion cells. . . .Part II concerns the methodology of classification. . . .many visual neurobiologists (myself included) have paid too little attention to the methodologies we have used in classifying nerve cells."

An absolutely crucial thesis of Stone, revolved around the concepts of "Single" and "Multiple" interpretations as a prefix to the term *variation* (page 58). Here, the single variation will be taken to indicate the primary variation, ***a single function describing an outcome based on a single input***. The multiple variation willl be taken as recognition that a specific outcome may involve a variety of parameters, only one of these parameters can be selected at one time to satisfy the single variation concept, ***with all other significant parameters controlled*** during the search for the single variation function .

Marshall & Zohar[4] pointed out in 1997; "...neuroscience covers many orders of magnitude, from molecules and subcellular structures to large systems, yet the discoveries of research workers at these different levels have so far not been integrated. For this to happen, we need not just more *facts*, but a more accurate overall *model*. This would require a conceptual breakthrough." **This work attempts to provide at least part of that breakthrough by leaning on the advice of Stone**. It deviates significantly from previous treatments in neuroscience and electrophysiology in recognizing the dominance of free electrons over ions in the operation of the neural system. It will be shown that ions play no significant role in the signaling operation of the visual and neural systems of animals.

> In pursuing a clearer understanding of the visual system, the author was astounded to find that there was no explanation of how the neural signaling system performed at the detail level. In analyzing the photoreceptor cells of vision, it became clear that this cell was a neuro-secretory cell and the same mechanisms employed in the signaling function of that cell were applicable to all neurons. Furthermore, the visual system could only be understood based on a complete understanding of the signaling processing capability of the neural system. It became necessary to expand this work to include a quite thorough analysis of the neural system as a subset.

To illustrate the situation more fully, the illumination range of the human eye extends over fifteen orders of magnitude. Similarly, the physical scale of the operating components of the visual system extends over eight orders of magnitude. Rodieck has provided an illustrative scale extending from the complete eye down to the p-orbital of the quantum physicist/chemist[5].

Although the author had been attempting to develop at least the concept of such an overall model of vision for many years while pursuing a peripheral vocation, his efforts to satisfy the call of Marshall & Zohar intensified during the last five years. By reexamining the fundamentals upon which the conventional wisdom was based, a truly conceptual breakthrough occurred that became a paradigm shift in thinking related not only to vision but the entire neurological system of biology. This paradigm shift brought into question each of a number of premises supporting the conventional wisdom. It is important to note that many of these premises within the conventional wisdom were never confirmed outside of a small community (a "school") located within a single large research organization.

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[3]Stone, J. (1983) Parallel processing in the Visual System: The Classification of Retinal Ganglion Cells and its Impact on the Neurobiology of Vision. NY: Plenum Press

[4]Marshall, I. & Zohar, D. (1997) Who's afraid of Schrodinger's cat? NY: William Morrow pp. 23-24

[5]Rodieck, R. (1998) The first steps in seeing. Sunderland, MA: Sinauer Associates, pg. 65

These organizations are typically "centers" or departments of universities where the residency is limited in duration for all but a few principals.

> The term "center" has begun to replace school because of its semantic concept. However, these centers should be considered relative centers, similar to relative maxima in calculus. They frequently exhibit a narrow perspective that conflicts with other centers. As an example, most centers promoting a trichromatic theory of vision are based on a framework (floating model) that is incompatible with those centers promoting a tetrachromatic theory of vision.

Because of these characteristics of the research environment, most of the premises within the common wisdom are never adequately challenged or confirmed independently by separate entities. Many of these premises were challenged and found wanting during the development of this work. Alternate proposals will be referenced in the following paragraphs. They form the core of this presentation, The Electrolytic, Tetrachromatic Theory of the Biological Visual System. This theory includes as an integral subset, The Electrolytic Theory of the Neuron (See **Section 8.1.3**).

While this work is not consistent with much of the theory considered the "common wisdom" within the vision community (see **Section 1.1.2** and additional references there), with rare exceptions it is consistent with all of the data in the literature. An example being where an investigator used a photometer in place of a spectrometer and proceeded to assign the photopic luminous efficiency function to the sensitivity profile of an individual spectrally-selective photoreceptor cell.

> In a more significant case, the data has been interpreted, based on the investigators heuristic background, to require an ion pump to transfer charge across a membrane and thereby generate a potential. Based on a more detailed model of the complete axon of a neuron and a broader knowledge of the field of electrostatics, it was found that electrical charge, separate from any atom, could be injected into the space within an axon in accordance with our current knowledge of semiconductor physics. With this realization, a more complete explanation of the data became available and the fundamental functional device/mechanism of the neuron was defined. This mechanism/device is the **Activa**™, the biological equivalent of the man-made transistor.

The analyses concerning the mechanisms related to the axon led to the development of a complete theory of the neural system based on a broader interpretation of the field of electrolytics. These analyses led to very detailed but alternate explanations of the operation of the neural system, based on the available data. It will be shown that the entire neural system, including the visual system is based on electrolytics.

Similar analyses uncovered alternate explanations for a variety of hypotheses within the common wisdom associated with biological vision. These included a quantum-mechanical explanation of the photoexcitation/de-excitation process in vision that did not rely upon the concept of stereoisomerism and provided precise descriptions of all four of the chromophores of biological vision. This explanation included the ultraviolet sensitive chromophore widely known to be used in insect vision but only recognized by a few as also used in chordate vision.

1.1.1 The definition of vision and blindness

A major problem surfaced early in this effort. There is no generally accepted definition of vision beyond the simple concept. Similarly, there is no generally accepted definition of blindness. At the conceptual level, blindness is obviously the lack of vision. However, this definition leads nowhere. Campion, Latto & Smith quoted Schneider in 1983 as saying[6]:

> "The term 'vision' subsumes a complex variety of processes, thus, for fruitful scientific discussion, a reference to 'vision' usually required further specification. Likewise, the term 'blindness' is not self-defining. An animal or patient showing what appears to be total blindness under one set of conditions may reveal considerable visual capacity in a different situation."

It is the goal of this work to provide a comprehensive theory and model of the biological visual and neural systems utilizing all of the available data **and** all of the scientific and engineering tools available during the 4th quarter of the

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[6]Campion, J. Latto, R. & Smith, Y. (1983) Is blindsight an effect of scattered light, spared cortex, and near-threshold vision? *Behav. Brain Sci.* vol. 3, pp 423- 447

20th Century. The top level model avoids the danger discussed succinctly by Wyszecki & Stiles[7]. It attempts to avoid any simplification that would void the model when explored at the detail level. This is done by insuring that all of the relevant parameters are properly interpreted in developing the subsidiary models. With such a top-level model, the definition of the degree of vision or degree of blindness experienced by an subject can be defined succinctly.

As will appear in Chapter 15, the functional system of vision can be subdivided into at least 100 individual feature extraction engines. These engines have the task of extracting information from the scene imaged by the eye. These engines do not work in series. While it is easy to define parallel paths in the initial stages of vision, and parallel modes of operation over defined portions of the system, the system is much more complex than any dichotomy can describe. At the cognitive level, the system architecture is that of a star-network of multiple points. Every engine is capable of talking directly to any other engine required, without going through a series of intermediaries. Recognizing the full architecture of the visual system allows specific failures, or abnormalities, to be isolated.

It is also possible, using the complete model of the visual system presented here , to explain many complex clinical syndromes. Achromatopsia is a good example. This condition presents a variety of individual diseases that can all be traced to a common error source within the Stage 1–Stage 2 interface of the visual system.

1.1.2 The order of exposition in this work

The subject of vision is so complex in its scope that care must be taken in developing a global discussion of the system responsible for it. This work will address the subject from a morphologically based framework, beginning with phylogenic details, then gross anatomy, et. cetera, until this framework ceases to be relevant. This point is reached in Chapter 5, while analyzing the photoreceptor cell, and marks the completion of **PART A** of the work. **Part B** consists of only two chapters, six and seven. It provides background material pertinent to the analyses in **PART A** as well further details related to the dynamics of the visual system from a variety of perspectives. **PART B** can be set aside if desired and treated as reference material. **PART C** consists of three chapters needed to understand the fundamental electrophysiology of the neural system. This material is critical to the understanding of the operation of the neural system supporting vision as well as other sensor and motor systems of the animal. **PART D** builds on the material of the previous parts to describe the operation of the visual system from the signaling perspective. This is the primary function of the neural portion of the visual system. However, the use of this term should not be confused with its use in biology to discuss the growth or global organization of the biological components of an animal. **PART E** concludes the formal part of the exposition by developing the relationships between the visual system and the performance descriptors used to describe its performance. This is done both mathematically and graphically. One chapter in this part, discusses some functional failures that result in well documented medical symptoms and syndromes. For a more complete summary of the content of these **PARTS**, see the **SYNOPSIS**. The Three-Level Table of Contents and the Index are also useful in locating areas of interest.

The following Table provides a summary of the Chapters of this work (some broken into Parts) and hyperlinks to the individual chapters/parts. Where a DOI number is given, a final version has been released. Where only a hyperlink to https://neuronresearch.net is provided, the material has been edited initially but may include some missing citations, etc.

> **The Table is easily searched using CTRL-F and a subject word**. Every Chapter concludes with its own searchable Table of Contents, List of Figures and Word Index.

[7]Wyszecki, G. & Stiles, W. (1982) Color Science, 2nd Edition. NY: John Wiley & Sons, pg 584

Chap.	Title	Scope	Address; DOI or in https://neuronresearch.net/vision/pdf/
1	Introduction, ***Phylogeny*** & eye configurations	Introductory with citations to specifics	(This document) 1Introduction.pdf
2	Introduction, Physical Environ., ***Order*** oriented,	Overview of environments & visual system optimizations	DOI: 10.13140/RG.2.2.35005.82409 2Environment.pdf
3	Description of **primate eye** and retina	Detailed description and interplay	3Description.pdf
4	Photo-Receptor/IPM/RPE complex of Chordate Eye	Cytology of photo-Receptor neurons	4Photoreceptor.pdf
5	**Photochemistry** of Biological Vision	Quantum–mechanical Photochemistry of vision	5Photochem.pdf
6	**Static Test Data** from Vision Research	Static properties of all neurons and neural groups	6Static.pdf
7	**Dynamics of Vision** including P/D Equation	Dynamic properties of detection, AP generation & eye motions	7Dynamics.pdf
8	**3-terminal neuron** of the 21st Century	Electrochem. of neuron operations in detail	8Electrochem.pdf
9	**Complex Neurons**; with functional parameters	Analog, phasic & hybrid neurons; synapses & noise	9Complex neurons.pdf
10	**Morphology** of the Neuron	Detailed look at the morphology of the electronic neuron	10Morphology of the neuron.pdf
10PtII	**Electrophysiology** of the Neuron	Time delays & measurements related to complex neuron circuits	10partII-electrophysiology.pdf
11	**Modeling** of biological phenomena	Functional blocks, schematic & circuit analysis techniques	11Biophenom.pdf
12	**Stage 1 Photodetection** Process in Humans	Details of the photodetection process and circuits	12Primary.pdf
13	**Stage 2 Signal Processing** –within the retina	Analog signaling, both additive & subtractive	13Secondary.pdf
14	**Stage 3 Signal Projection** used throughout modality	Signal encoding, transmission & decoding, specifics of	14Tertiary.pdf
15Pt1	**Higher Level Perception**; signal interpretation Pt 1	Spatial, shape, intensity & color; similarity to television	15Higher Level Pt 1.pdf
15Pt2	Higher Level Perception; Pt 2Information extraction	Thalamic & cortical roles in vision; role of the pulvinar	15Higher Level Pt 2.pdf
16	Equations of Vision & their confirmation	More complex equations than easily developed in a chapter	16Equations.pdf
17Pt1a	**Luminance, chrominance** descriptors of Vision;	"Rods" as an archaic concept; problems with CIE concept	17Performance Pt 1a.pdf
17Pt1b	**More on chrominance**. descriptors of Vision;	Introduction of the Chromaticity Diagram (2016) & comparisons	17Performance Pt 1b.pdf
17Pt2	**Temporal and Spatial** descriptors of Vision	Rates of motion and underlying principles supporting stereopsis	17Performance Pt 2.pdf
18	**Visual Abnormalities** & Clinical Electrophysiology	Intertie with clinical medicine; broad range of subject matter	18Anomalies.pdf
19	**Reading/Scene Analysis** & Object Recognition	Details of scene analysis and mechanisms of reading	19Reading.pdf
20	Different Theories of Vision Comparing	Brief discussion of other more fragmentary theories	20Alternate theories.pdf

To aid in the exposition, each chapter contains an introductory section(s) developing the background needed to understand the presentation in detail. This material frequently contains both a discussion and a glossary specific to that chapter. All of the terms in these glossaries are assembled in the main glossary of the work.

The following Table provides a summary of the Appendices associated with this work. Many appendices were prepared as working documents during the preparation of this work. They are not presented here but *may* be found at https://neuronresearch.net . Only those of general interest are found in the following Table. Where a DOI number is given, a final version has been released. Where only a hyperlink to https://neuronresearch.net is provided, the

material has been edited initially but may include some missing citations, etc.

The Table is easily searched using CTRL-F and a subject word. Every Appendix concludes with its own searchable Table of Contents, List of Figures and Word Index.

Appen.	Title	Scope	Address; DOI or in https://neuronresearch.net/vision/pdf/
A	**Photoexcitation/ De-excitation Equat**.	Complete Solution to the Photoexcitation/De-excitation Eq.	Appen A P_D.pdf
B	The Circuitry of the Neuron	The fundamental circuitry within the basic electrolytic neuron	Appen B Neurocircuitry.pdf
F	**The Rhodonines**–the Chromophores of Vision	Extraction & Characterization of Visual Chromophores--Rhodonine	Appen F Rhodonine.pdf
G	**Pantone & other color** spaces vs Chromaticity	A comparison of "color wheels" vs the Chromaticity Diagram (2016)	Appen_G_Pantone_vs_Chromaticity.pdf
J	**Dolphins Vision** System	Description of the unique visual system of Dolphins	Appen J Dolphin Vision.pdf
K	The Standardized Human Brain	A brief description of the Human Brain from the visual perspective	Appen K Standard Brain.pdf
L	The STANDARDIZED HUMAN EYE	A comprehensive tabulation of the properties of the Human eye	DOI: 10.13140/RG.2.2.16200.26883 Appen L Standard Eye.pdf
M	The **Standard Neuron**	A compilation of features and Mechan.of the electrolytic neuron	Appen M Standard Neuron.pdf
O	The **Serape Graph**	A valuable method of display for Complex electrolytic circuits	Appen O Serape representations.pdf
ZA	**Chromaticity Diagram** (2016)	A New Chromaticity Diagram representing perceived color	Appen ZA Chromaticity Diagram (2016).pdf
ZB	**Luminous Efficiency** Function (2016)	A New Luminous Efficiency Function based on real measure.	Appen ZB Luminous_Efficiency Fct
ZC	**Stereographic vision** (2017)	First explanation of stereoscopic vision based on physiology	Appen ZC Stereo_Vision_(2017).pdf
ZD	**Visual Snow**, VS	A survey and report on several Hundred sufferers of visual snow	Appen ZD Visual Snow.pdf
ZF	**Detached Retina diary** & its repair	Detached Retina: A Unique Diary Including its surgical repair	DOI: 10.13140/RG.2.2.26535.39841 Appen ZF_Detached_Retina_Repair.pdf
ZG	**Schematic Human Eye** (2016)	An updated compendium of the eye, including the field lens	Appen ZG Schematic Eye (2016).pdf
ZH	**Pulvinar**, Critical role equal to that of Area 17	Critical Role of the Pulvinar in good Human Vision	DOI: 10.13140/RG.2.2.30918.42568 Appen ZH_Pulvinar_CriticalRole.pdf
ZJ	Visual capability of a **Subject with no Area 17**	Analysis of the phenomenal vision of one without visual cortex	Appen ZJ Analysis of Subject B_I_.pdf

Items not Hyperlinked remain in draft form. For those interested in an item, it is available from the author at jtfulton@neuronresearch.net

1.1.2.1 The order of exposition in this chapter

Because of the broad scope of this work, it is useful to provide an overview of it in a superficial introduction. This chapter is designed to provide that overview without a complete list of supporting material. However, the reader will find internal references to complete discussions of individual topics that include encyclopedic references to the pertinent data, and where available to the prior conventional wisdom.

The chapter begins with a broad discussion of the role of vison in evolution within the biological kingdom. In **Section 1.2**, a phylogenic tree is provided that uses vision as one of its underlying parameters. Based on this tree, it is possible to organize and categorize the myriad eyes found within the animal kingdom based on morphology (and interestingly on the various forms of Vitamin A). This phylogenic approach leads to the demonstration that all eyes have evolved from a common ancestor. It also leads to the definition of three fundamental forms of eyes that can be individually related to the major phyla within the animal kingdom, the *Arthropoda, Mollusca and Chordata*.

The phylogenic discussion sets the stage for formulating the philosophy, perspective and methodology used to prepare the rest of the work. However, it is necessary to present some additional background in a non confrontational atmosphere before proceeding. **Section 1.3** presents this background. It focuses on a number of conflicts between the common wisdom frequently expressed within the literature of vision at the end of the 20th Century and some simple observable facts. If the reader keeps these observable facts in mind, it may be easier to accept the following paradigm shifts on first reading.

Section 1.4 is introduced to highlight some of the scientific difficulties related to the common wisdom apparently shared by a large fraction of the vision community at the end of the 20th Century. A variety of serious problems related to current and past experimental laboratory techniques are discussed. Many of these relate to the lack of adequate control of the parameters underlying and controlling the processes being investigated.

Section 1.5 provides a top level view of the theory and model of this work **and** provides a list of the major (and multiple) paradigm shifts leading to a comprehensive understanding of the biological visual system.

Section 1.6 provides a superficial validation of the proposed theory and model (that is supported within the main body of the work). This validation focuses specifically on human vision but applies to all biological vision with the appropriate change in parameters. It includes the first comprehensive theory, model and performance descriptors of color vision, the first comprehensive theory, model and reinterpretation of the adaptation process, the first end to end description, theory, and model of the neural system and many other lower level findings.

Section 1.7 provides a more comprehensive introduction to the subsystems of the eyes found in the major animal phyla using some of the concepts developed in **Sections 1.5**

Section 1.9 concludes the chapter with a review of the major findings of this work.

Before proceeding to these main subject areas, **Section 1.1.2** introduces some initial terminology required to interpret the remainder of the Chapter. Later, **Section 1.2.4** will present some important recommendations regarding morphological nomenclature following the discussion of phylogenics. The reader is also referred to **the comprehensive Glossary** in the rear of this text as well as **the Description of a Standard Human Eye** that incorporates the myriad of parameters crucial to the operation and understanding of the visual process. A similar Description of **the Standard (and variations on the) Neuron** is also provided.

1.1.3 Terminology

It should be noted here that terminology is an almost overwhelming problem in vision research. "As discussed in Rowe & Stone (1977) as well as by others, there is an unfortunate tendency for role-indicating names to lead to fixed ideas about function, in contrast to those that are more neutral and adaptable to new findings[8]." This is doubly unfortunate as Rockland, et. al. also note; "terminology also reflects, and, even more, guides ways of thinking about the visual system as a whole." This has been particularly unfortunate in the adoption of a morphological description of photoreceptors to describe their putative spectral sensitivity.

Different isolated groups have chosen to adopt floating models and use expressions in absolutely arbitrary ways. One of the simplest examples deals with "red," "green" and "blue" rods. One school uses these terms to show the

[8]Rockland, K. Kaas, J. & Peters, A. (1997) Cerebral Cortex, Volume 12. NY: Plenum Press pg vii

region of the spectrum where these entities absorb maximally; the other school uses the same terms to indicate the apparent color of the entities as observed by the investigator. The second school assumes that the entity absorbs maximally in the part of the spectrum complementary to its name. Both schools are obviously avoiding the question of why there are color sensitive rods if there are also color sensitive cones.

Because of the terminology problem, ***an extensive Glossary is included at the end of this work***. Every effort will be made to maintain compliance with the definitions in that Glossary. Similarly, in this work, a word or expression means exactly what the author wants it to mean, in conformance with the Glossary. Conflicts with other authors' terminology should be considered a cultural matter, not necessarily a difference in science. As an example, in this work, a photosensitive spot without an accompanying optical aperture will not be considered an eye. The simplest possible eye, a single ommatidium, consists of a photoreceptor cell inside a light tight enclosure with a single aperture. The aperture may be open as in the primitive *nautilus* but more generally includes a lens, which is, *de facto,* an optical element filling an aperture. Semantically, a light tight enclosure containing only one aperture is a *camera*.

1.1.3.1 Spectral appearances

This work will provide a definitive discussion of the four chromophores of vision derived from Vitamin A_1 The total rises to twelve if you include the chromophores derived from Vitamin A_2 and Vitamin A_3. The spectral peaks of the set of chromophores of each type are so close that there is no known difference between them in the visual spectrum. In this work, the following relationships apply:

Chromophore Name	λ	absorbs maximally Narrow band name	appears to observer Broad band name
Rhodonine(5)	625 nm	Reddish-Orange	Cyan, a greenish blue
Rhodonine(7)	532 nm	Yellowish-Green	Magenta, a purplish-red
Rhodonine(9)	437 nm	Purplish-Blue	(Unsaturated) Yellow
Rhodonine(11)	342 nm	--	Transparent to humans

The narrow-band names are taken from the widely published CIE 1961 Chromaticity Diagram. The appearance of the mixture of these chromophores to humans is dominated by the purplish-red of Rhodonine(7). The narrow band compliment to 625 nm, i. e., 494 nm is named aqua in this work. The narrow band compliment to 437 nm, i. e., 572 nm is named (saturated) yellow in this work.

Besides these primary absorption peaks associated with the chromophores, there are two perceived spectral response peaks resulting from computation in the cortex. They appear at 494 nm and 580 nm, the later associated with the so-called Purkinje shift. In the past, the community has not been able to differentiate between perceived spectral maxima due to actual absorption and those due to cortical computation.

1.1.3.2 A process

From another perspective, the anatomist has grown to use the term process to mean a structure related to an animal or cell. This use of the word conflicts quite seriously with the more general use of the word in science and engineering where process is associated with an operation. The latter interpretation will be the way the word is used in this work.

1.1.3.3 Summation and addition

A situation is encountered in psychophysiology wherein the term addition is "the cooperation of subliminal effects in such a way that the total effect is supraliminal." This work will be exploring the neural system at levels of detail that require more precise terminology. It will define a variety of thresholding functions that determine precisely whether a signal is subliminal or not. Addition will be used in the normal mathematical sense. In this sense, the addition of two subliminal effects at the input to a thresholding circuit may produce a resultant effect that is supraliminal or is suppressed (remains subliminal) depending on the threshold of the circuit. In either case, the resultant is easily recognized electrophysiologically. Cooperation implies a willful process and is not appropriate at the neural level.

1.1.3.4 Standardization of cytological names.

The names used to describe various eyes originally arose through different investigators operating in relative

isolation under primitive conditions of microscopy. Strausfeld & Nassel[9] have recognized this profusion of overlapping terminology in their area of interest, the neural connections between the eye and brain. They have recommended that the terminology used for insects in this area be adopted *in-toto* for the crustaceans, both being families of *Arthropoda*. This work will provide a broader matrix of terminology equating that used most frequently in research on Arthropoda, Mollusca and Chordata. **Section 1.2.4** will suggest and adopt a standard terminology that can be used across all Phyla when discussing vision.

With morphology, histology and cytology involving mainly static examinations of materials, there is a problem with one of the term used-- evagination. This is particularly true of neural material. Various structures on the periphery of a cell are labeled evaginations, i. e., a body part on the outside of a material because of eversion (the act of turning inside out) of an inner surface. Neurons are members of a class known as neuro-secretory cells. They can secrete proteins onto their external surfaces. This results in an extracellular structure that is intimate with but not a part of the living cell. It appears that the noun evagination should frequently be replaced by secretion, especially when discussing the tubules and disks associated with photoreceptor cells. The term secretion is frequently used when examining mechanoreceptors. These cells are very similar to the photoreceptor cells which are also neuro-secretory.

Regarding anatomy, and more specifically, morphology and cytology, the investigator attempts to understand how some tissue or structure is built and used based on his personal experience and training. This can become a barrier to progress if the investigator does not have a sufficiently broad background to recognize the attributes of a situation. As an example, morphologists trained in the biological arts have not been able to define the purpose or function of the Node of Ranvier associated with a neuron. However, to an investigator trained in signaling theory and electronics, its purpose is patently obvious, especially when examined with an electron microscope. The Node of Ranvier is a conventional signal repeater of a simple electronic type; it is a biologically based three terminal transistor amplifier.

1.1.3.5 Elementary optical assemblies

This work defines a simple ommatidium as the “fundamental eye.” It incorporates all of the basic elements required to constitute a physical eye. This fundamental eye can be incorporated into a variety of configurations. Some of these configurations involve treating the optical portion and the photosensitive portion differently or separately. The ommatidium normally exhibits a long slender aspect ratio. As will be seen below, even this normal aspect ratio can become considerably larger.

The simplest modification to the fundamental eye is to separate these two portions along the optical axis. This results in an expanded fundamental eye or expanded ommatidium as found in *Copilia*. If the photosensitive part, the rhabdom, of the fundamental eye is replicated directly behind a single lens constituting the optical portion of the eye, an eye is formed that is named an ocellus. If this replicated photosensitive assembly is now separated spatially from the optical assembly, the resulting eye is functionally an expanded ocellus. It is called a complex eye and the photosensitive portion is called a retina (of the direct type). An alternate development of the fundamental eye is to replicate the entire ommatidium as a unit. The resultant eye is the compound eye. All of the above eyes are readily traced through the phylogenic record of *Arthropoda* and *Mollusca*. There is an alternate form of the expanded ocellus found in the phylum *Chordata*. It involves a complex eye as defined above but with the retina physically reversed relative to the light path. Although this configuration can be easily derived from the early photospots of *Planaria*, the eye is one of the most difficult features to preserve over time and the possible intermediate forms have not been documented in the archeological record.

These basic forms have been adapted and extended in every possible way to satisfy ecological needs, including a catadioptric optical system illuminating two back to back direct retinas in one eye (the mollusc, *Pecten*).

1.1.3.6 Fundamental mounting arrangements

The eyes defined above have been packaged in a wide variety of ways in the animal kingdom. There are three ways that are of primary importance. The eyes of Arthropoda are invariably *body mounted* to a much larger structure, usually either a head or a carapace. There is no relative motion between the eye and the associated body part. The neurons from the eye leave its rear surface over a relatively large area and proceed to the optic lobe of the brain. The molluscs follow the same approach except in the case of the most advanced forms. In these forms, an attempt is made to reduce the cross-sectional area of the neuron bundle leaving the eye (at least in one plane). This is done in

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[9]Strausfeld, N. & Nassel, D. in Autrum, H. (1981) Comparative Physiology and Evolution of vision in invertebrates--B; Invertebrate visual centers and behavior I. NY: Springer-Verlag pg. 5

order to provide a small amount of *one dimensional angular freedom* between the eye and the head. The head also exhibits some angular freedom relative to the body. These animals are not believed to employ projection neurons to aid in this process. The chordate eye has advanced even further. It employs projection neurons and a sophisticated spatial encoding process to reduce the diameter of the optic nerve bundle dramatically. This allows the eye to be mounted so as to achieve *two-dimensional angular freedom* of a significant degree relative to the head. In the higher forms of this phylum, the head also exhibits considerable angular freedom relative to the body.

1.1.3.7 Specific bibliography

When discussing the eye, it is important to recognize that the term cuticle is used variously in a variety of biological disciplines. In the vernacular, it is the hardened portion of the skin around the finger and toe nails. It is used for any area of *hardened cellular structure* in many works, a synonym for the epidermis. However, the eyelid in primates does not qualify as a hardened portion of the skin. The cornea does. In more general zoology, it refers to any *non-cellular* hardened or membranous covering of many invertebrates. It is generally extremely thin. There is a similar problem with conjunctiva. It is usually described as a mucous membrane lining the inner surfaces of the eyelid and the outer surface of the eyeball. This membrane is extremely thin in the area of the cornea and consists primarily of five or six layers of squamous cells. It exhibits no structural strength. It is more properly called the corneal epithelium in this region.

1.2 Animal phylogenics with vision as a fundamental parameter

This section will use the term phylogenics when discussing the ancestral history of organisms based on their morphological characteristics. This usage stresses the separation from phylogenetics, studies seeking to show the genetic relationship between species. At this time phylogenetics has not addressed subjects like convergent evolution, which play a role in the following material. Both terms are adjective forms of the noun phylogeny. Ptacek & Hankison have addressed the complex subject of species delineation in Ruse & Travis[10].

The conventional phylogenic tree of *Chordata*, although subject to continuing modification, is not significantly impacted by major variations introduced by the visual modality. On the contrary, the conventional phylogenic tree of Insecta takes on an entirely new dimension when the highly diverse forms of the visual modality of the species included in that phylum are placed in perspective (**Section 3.6**). The employment of three different forms of vitamin A in the generation of the retinines (with an i to distinguish their unique resonant diol character)forming the chromophores of vision is found to spread across wide swaths of both the chordate and insect Phyla.

1.2.1 Animal evolution categorized by visual configuration

Waehneldt has provided a phylogenic tree that begins with the ancestral flagellate stock around 600 million years ago[11]. His discussion traces the evolution of myelin, an important component of the neural system and therefore of fundamental interest in studying the visual system of *Chordata*, although myelin does not appear to play a significant role in the visual system of *Insecta*. Wolken has provided a time line of evolution that he credits to Calvin (1969)[12]. This figure puts evolution with respect to vision in perspective. Primitive vision, spatial sensitivity to light, began well before the evolution of *Chordata*. Interestingly, the chordates began with the fish, some 470 million years ago. This is at least 150 million years before the age of reptiles and 250 million years before the age of dinosaurs. Mammals are a Johnny-come-lately on this time scale.

In examining any zoological description of the animal kingdom, one finds that all the basic geometric symmetries have been used and even the lowest and oldest forms of life exhibited some sensitivity to irradiance. Simple animal structures may be based on point symmetry, line symmetry and plane symmetry. Until the time of the early worms, the sensitivity to irradiance was more aligned to the non-imaging aspects of solar irradiation than it was to what we would now define as the principal purpose of eyes, discerning images. The early worms, which evolved more than 600 million years ago and are still with us today, were the first bilaterally symmetrical animals, i. e., symmetrical about a plane. The planaria, *dugesia tigrina*, exhibited a curved row of photoreceptor cells on each side of the anterior part of its body next to another curved row of cells which formed a barrier. No other optical element was associated with this system. The planaria could sense the direction of the source of illumination and/or changes in

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[10]Ptacek, M. & Hankison, S. (2009) The pattern and process of speciation *In* Ruse, M. & Travis, J. *eds*. (2009) Evolution: The First Four Billion Years. Cambridge, Mass: Harvard Univ Press pp 177-207

[11]Waehneldt, T. (1990) Phylogey of Myelin Proteins *Annal NY Acad Sci* vol 605, pp 15-28

[12]Wolken, J. (1975) Photoprocesses, Photoreceptors, and Evolution NY: Academic Press pg 9

that illumination by the way the photoreceptor cells were shadowed.

1.2.1.1 A Phylogenic Tree

Taxonomists have struggled mightily in organizing the animal kingdom by familiar traits. They have usually considered about 12 different traits as important. By selecting these traits in different order, they have constructed many family trees representing the evolution of all animals from a single cell ancestor. A sequence that has been useful and widely published is:

+ Type of symmetry

+ Presence or absence of a coelom, an intestinal tract

+ Presence or absence of a digestive system

+ Type of skeleton

This sequence has led to the widely recognized dichotomies, vertebrates versus invertebrates OR chordates versus non chordates OR internal versus external skeletons. These descriptions satisfy the human penchant for describing things in terms of dichotomies. The above dichotomies are frequently taken as approximately synonymous. Man's penchant for defining things in terms of dichotomies is so strong, it extends to dividing all animals into two major classes Protostomia and Deuterostomia, which basically conforms to non-chordates and chordates. A phylogenic tree exhibiting this division represents the diphyletic theory of phylogeny.

A problem exists in defining skeletal types in the above way; three different types actually exist. An animal can have an internal skeleton, an external skeleton OR no skeleton. This situation which is described as a trichotomy. A similar situation exists with respect to visual systems as defined in this work; there are four types, a quadrichotomy, if one includes photospots.

For this discussion of phylogeny, the technical names used will follow the overall terminology of Hickman[13]. While probably dated in the eyes of many, Hickman is at least consistent. A more global taxonomy has recently become available through an international cooperation. http://www.itis.gov/ItisDataTools/jsp/hierarchy.jsp provides a comprehensive hierarchal list from Kingdom through Order (or other windows) using a comprehensive set of tools and tables.

Figure 1.2.1-1 illustrates a phylogenic tree, based on the sequence given above but recognizing the three skeletal types. This tree also illustrates another important feature, the type of eye involved. This figure shows *chelicerata xiphosurida* (at upper left) distinct from the rest of the crustaceans for two reasons; first, because of their apparently unique anatomical character. Second because of the amount of information available for the horseshoe crab, *Limulus*.

[13]Hickman, C. (1970) Integrated principles of zoology. 4th Ed. St. Louis MO: C. V. Mosby

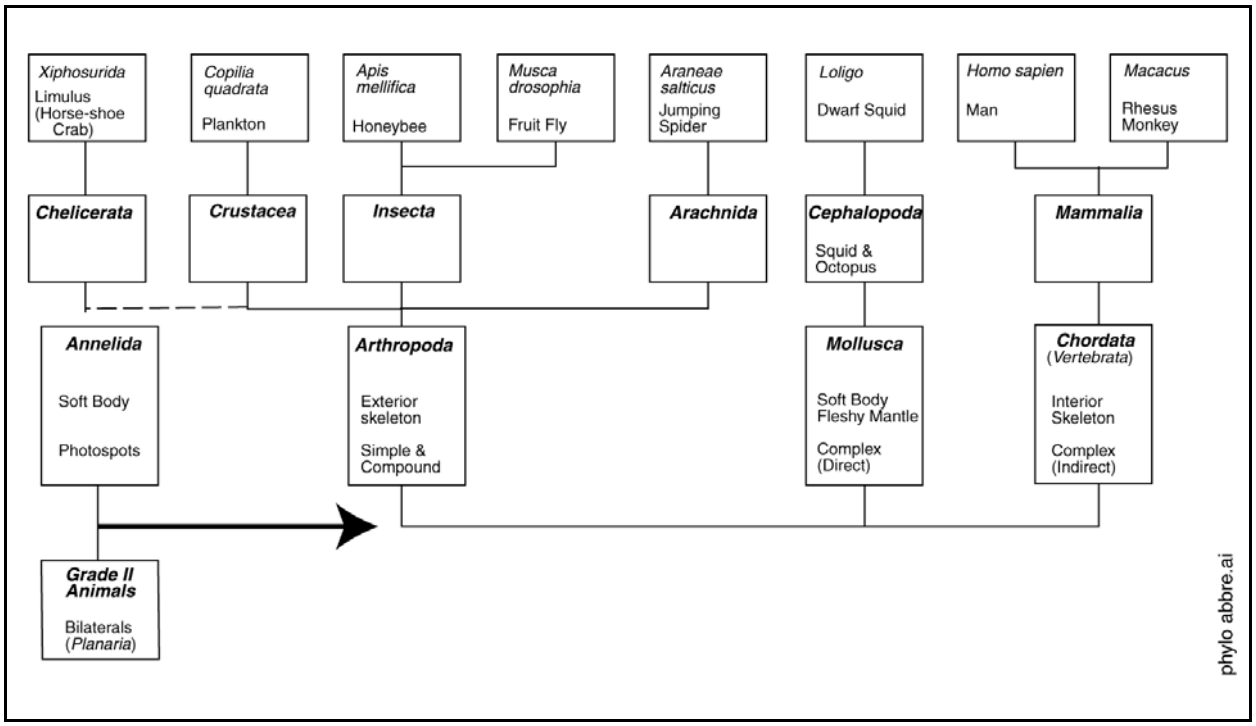

Figure 1.2.1-1 An abbreviated Phylogenic Tree focused on the visual aspects of taxonomy. All of the animals shown are bilaterally symmetrical. All of the animals to the right of *Planaria* have a coelom. As indicated by the subtitles below the title in the box of each phylum, each phylum has a different body structure and each phylum has evolved a functionally and structurally different visual system. *Planaria*, *Copilia* and *Limulus* evolved in paleontological times but are still available for study. Also noted are the names of other species that have played a major role in the literature of vision. *Copilia* and *Araneae* are the only animals with photoreceptors scanning separately from and behind their lens.

Most taxonomies show rapid evolution of animal types following the emergence of the bilateral and unsegmented worms, typified by *Planaria*. This creature was, and still is today, sensitive to light as will be discussed later. With the development of an intestinal tract, coelom, four major Phyla within the designation Eucoelomata competed for their place in the environment, the Annelida, the Arthropoda, the Mollusca, and the Chordata. The Annelida and Mollusca are soft bodied animals without a skeleton. The Arthropoda are characterized by an exoskeleton and the Chordata evolved an internal skeleton as represented by Vertebrata. Each of these Phyla evolved a different visual mechanism. Annelida (the segmented worms) remained primitive, exhibiting only a photospot like the *planaria*.

There are a wide range of names used to describe the different types of eyes. Usually an author is discussing only a subset of the eyes found in the animal kingdom. Sometimes, he is painting a conceptual picture of possible eye configurations as an introduction[14]. This work will define a set of names compatible with the entire kingdom and based primarily on topology (See **Section 1.2.4**). In this scheme, the simplest light detector, the photo-spot is not an eye in that it has no defining optical aperture. The first topographically complete eye is the ommatidium, a convergent optical element with a photosensitive cell at its image plane. A single ommatidium will be called a simple eye in this work. There are two primary methods of increasing the visual performance of the ommatidium. The total assembly can be replicated into what is known as a compound eye. Alternately, the photosensitive element can be replicated behind a single optical aperture into a complex eye.

The label under each Phylum, in the above figure, describes the type of visual system used in that Phylum. In a major sense, the Simple and Compound eyes are the same, only varying in degree of replication. The term Complex eye is introduced here for eyes containing a large scale retina behind a single optical system. There is a further subdivision of this term. Complex eyes exist where the incident illumination falls first on the distal ends of the photoreceptor cells (the direct retina) and those where the illumination falls first on the proximal ends of the

[14]Oyster, C. (1999) The Human Eye. Sunderland, MA: Sinauer Assoc.

photoreceptor cells (the inverse retina). The orientation of the retina is a major difference in visual systems as will be developed later. The primary operational difference is in the mounting of these complex eyes. The complex eye with a direct retina is used in body mounted eyes. The inverse retina is used in eyes that can move independent of the head, i.e., orbital eyes.

The top row of the figure includes the common and a (generic) family name for many animals that have played a major role in vision research. Although *Copilia* has not played a major role, it has highlighted an eye that has not proved sufficiently useful to evolve further. However, the mechanism used is found in the more sophisticated members of *Chordata* where it has been expanded to provide both saccadic and tremor motions. The continued existence of *Planaria* and *Limulus* are of great value in understanding the evolution of vision in animals. The unique characteristics of *Limulus* have aided considerably in the development of this work. Its visual system will be explored in detail in Appendix D.

During the 1960s and 1970s, there was a spirited discussion of phylogeny based on the type of photoreceptors employed. This activity relied heavily on the ultrastructure of the cell without concern for how the photoreceptor actually created an output signal. Eakin proposed a biphyletic approach, Vanfleteren & Coomans promoted a monophyletic approach and Salvini-Plawen & Mayr supported a polyphyletic (but fundamentally a triphyletic) approach. Others have adopted a lunch room menu approach in attempts to describe the configuration of all eyes following adaptation into a variety of environmental niches. These possibilities were discussed by Leutscher-Hazelhoff in a short essay[15]. **Chapters 4** and **12** will focus on a triphletic approach that is compatible with the phylogeny in the above figure based on the complete eye.

Figure 1.2.1-2 provides a more detailed phylogenic tree based on a fifth trait, the molecular form of the retinoids found in the animals, and additional data on what retinoids have been found in the most primitive animals. The bottom row of the chart should only be considered illustrative. With the recent discovery of the hyperthermophiles (primarily tube worms at the bottom of the ocean near hot water vents), the most recent classification of life contains three branches[16]. The first and possibly oldest is *Archaea*. It is a prokaryote that does not rely upon oxygen in its metabolism (the hyperthermophiles). The second is the oxygen loving prokaryotes, the *Bacteria*. The third is the eukaryotes that includes the plant and animals. In this arrangement, the *Algae* and *Fungi* are considered plants. Protozoa remain grouped with the animals.

Land & Nilsson have provided a similar phylogenic tree stressing different parameters for a more popular audience[17]. As an example, they did not develop the role of different variants of vitamin A used by different species and the role of these variants during the lifetimes of catadromous and anadromous fish.

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[15]Leutscher-Hazelhoff, J. (1984) Ciliary cells evolved for vision hyperpolarize-Why? Naturwissenschaften, vol. 71, pp 213-214

[16]Krauss, L. (2001) Atom: an odyssey from the Big Bang to life on Earth. QB981.K77 2001

[17]Land, M. & Nilsson, D-E. (2002) Animal Eyes. NY: Oxford Press Page 14

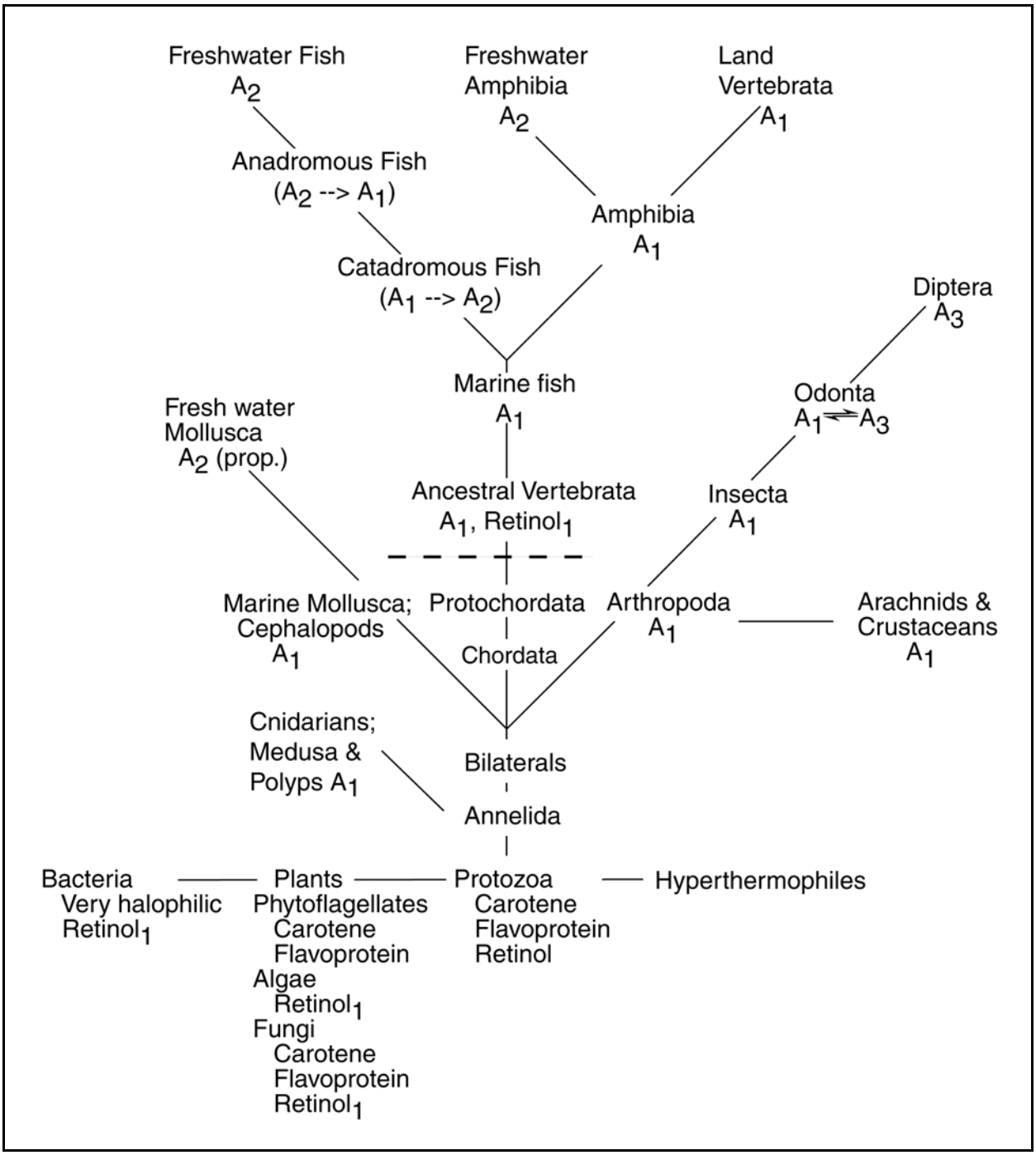

Figure 1.2.1-2 Phylogenic relationships tracing the presence of Vitamin A in various families and species. Note the presence of Vitamin A_2 and A_3 but the predominance of Vitamin A_1. The form of the vitamin used appears to depend on the environment. The chart varies considerably from that of other investigators. Several authors use the horizontal dashed line to separate vertebrates from invertebrates . Only the phylum *Chordata* is reasonably completely documented.

Different variants of this chart have appeared in the literature for the last 30 years[18]. This chart differs significantly from those versions and incorporates the findings of Vogt[19]. He demonstrated that a third retinoid was important to the vision process in parts of *Arthropoda*. This form is based on the 3-hydroxyretinol molecule and has been labeled Vitamin A_3. See **Section 5.3.3**. The 3-hydroxyretinol form is found in decaying plant matter originally based on Vitamin A_2.

Recently, a fourth form of Vitamin A has been reported. It has only been reported in one species by one research team. This form is based on 4-hydroxyretinol and was reported in a bio-luminescent squid, *Watasenia scintillans*. No etomology was provided for this unusual situation. This form was not found in 20 other types of squid found in the same location by the same team. It is conceivable that the animal eats material derived from decaying plant matter originally based on Vitamin A_1.

The figure demonstrates the fact that very few orders, families and species rely on the A_2 form exclusively. Only one large order relies upon the A_3 form of Vitamin A. It is too early to discuss the prevalence of the A_4 form. It may be confined to deep ocean specimens.

The figure also shows that there are a variety of animals that employ different derivatives of Vitamin A in the Outer Segments of their eyes at different times in their life. It also provides a dividing line between vertebrates and invertebrates and includes the interesting case of the invertebrate chordates (protochordates) which will be discussed in **Section 1.2.1.5.2** and cartilaginous chordates (sharks) discussed in **Section 1.2.1.5.3**. All living terrestrial vertebrates indicate their marine parentage in the presence of, and reliance on, Vitamin A_1 in their tissue. For continuity with other similar diagrams, it continues to show the Anadromous and Catadromous Fish. These fish live in one environment for a majority of their existence but move to the other environment for spawning, usually followed shortly by death. Whether moving into the other environment is a major factor in the demise of the fish will not be explored here. However, these animals do exhibit both Vitamins A_1 and A_2 in their tissue after changing environment. A similar situation is found in Donata with regard to the Vitamins A_1 and A_3. Some of the earlier literature has implied an evolution from Vitamin A_1 to Vitamin A_2 followed by a retrogression back to Vitamin A_1 on the way to the terrestrial vertebrates. This appears to be unnecessary.

Martin has provided a remarkable review of the light sensitive properties of the phylum *Cnidaria*, jelly-fish and polyps[20]. These are radially symmetrical animals and believed to be the simplest multi-cell animals. Martin shows the many simple animals of this phyla employed a variety of eyes sharing many of the specific features now found in the eyes of *arthropoda*, *mollusca* and *chordata*. Specifically, short wavelength trichromatic vision was achieved using medium wavelength, short wavelength and ultraviolet wavelength photoreceptors. The photoreceptors employed disks in an outer segment with nine dendrites forming a chalice around the disks as in *Chordata*. However, the retina was not inverted as in *Chordata*, but like that of *Mollusca*. The eyes of *cubomedusae* resemble that of *nautilus*. Neurologically, however, the system employs neural signaling analogous to that of *Chordata*. It is not clear when the individual members of this phylum evolved and their soft bodies make it difficult to determine from the fossil record. Being strictly marine animals, it can be assumed they were Vitamin A_1 based.

The literature contains a number of references to the remarkable convergence of the chromophores found in the three types of eyes[21]. On the contrary, this work suggests a remarkable degree of commonality but little convergence in the common meaning of the term. The assumption here is that the chromophores did not converge but actually diverged, from an original Vitamin A_1-based chemistry, based on adaptation to particular environmental conditions. See **Section 5.2.3**.

Figure 1.2.1-3 provides a mapping of the evolution of animals from the sea into two major and one minor "niches." The map is incomplete but establishes some important guidelines. All of the marine-based families, including the bulk of the terrestrial mammals, have saline-based blood and utilize Vitamin A_1. They are all capable of, but some may not employ, tetrachromatic vision. When migrating to freshwater aquatic environments, the families retain their tetrachromatic capability but now employ Vitamin A_2 in growth and vision. This has caused no significant effect on the spectral response of the animal.

Recent experiments have shown the utilization of one form of vitamin A may not be to the complete exclusion of all

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[18]Wald, G. (1970), also Wolken, J. (1975, 1986, 1994)

[19]Vogt, K. (1989) *In* Stavenga, D. & Hardie, R. *ed*. Facets of Vision, NY: Springer-Verlag, Chapter 7

[20]Martin, V. (2002) Photoreceptors of cnidarians Can J Zool vol 80, pp 1703-1722

[21]Birge, R. (1981) Photophysics of light transduction in rhodopsin and bacteriorhodopsin. *Ann. Rev. Biophys. Bioeng.* vol. 10, pp 315-354

others. Torma & Valquist have found significant levels of Vitamin A_2 in mouse liver[22]. The amount was only a few percent of the Vitamin A_1 present and appeared to be a stable percentage regardless of diet. According to Vogt[23], Diptera may have evolved to a Vitamin A_3-based system due to the limited availability of sources of Vitamin A_1 in its diet. **Section 3.6.4** also shows that *Lepidoptera* (butterflies and moths) probably use vitamin A3.

When migrating to a non aquatic environment, there is a significant impact on vision in several families. In *Arthropoda*, there appears to be a loss of long wavelength spectral sensitivity in many families, possibly related to the fragility of the L-channel chromophore and the incubation temperature of many insects. In *Chordata*, there is a loss of UV-channel spectral sensitivity for a different reason. The increased thickness of the tissue portions of the optical system causes an absorption of the ultraviolet light before it reaches the retina, even though many retinas remain sensitive to the ultraviolet. Rodieck has noted that many small terrestrial chordates, he mentions rodents, exhibit significant ultraviolet sensitivity[24]. This is to be expected due to the physically shorter path traveled by the light in reaching the retina. In many situations, there are animal families that can exist in two distinct environments, on either a transient or continuous basis. These families have frequently evolved unique physical adaptations to satisfy the different environmental requirements associated with either the salinity change or the change in index of refraction involved.

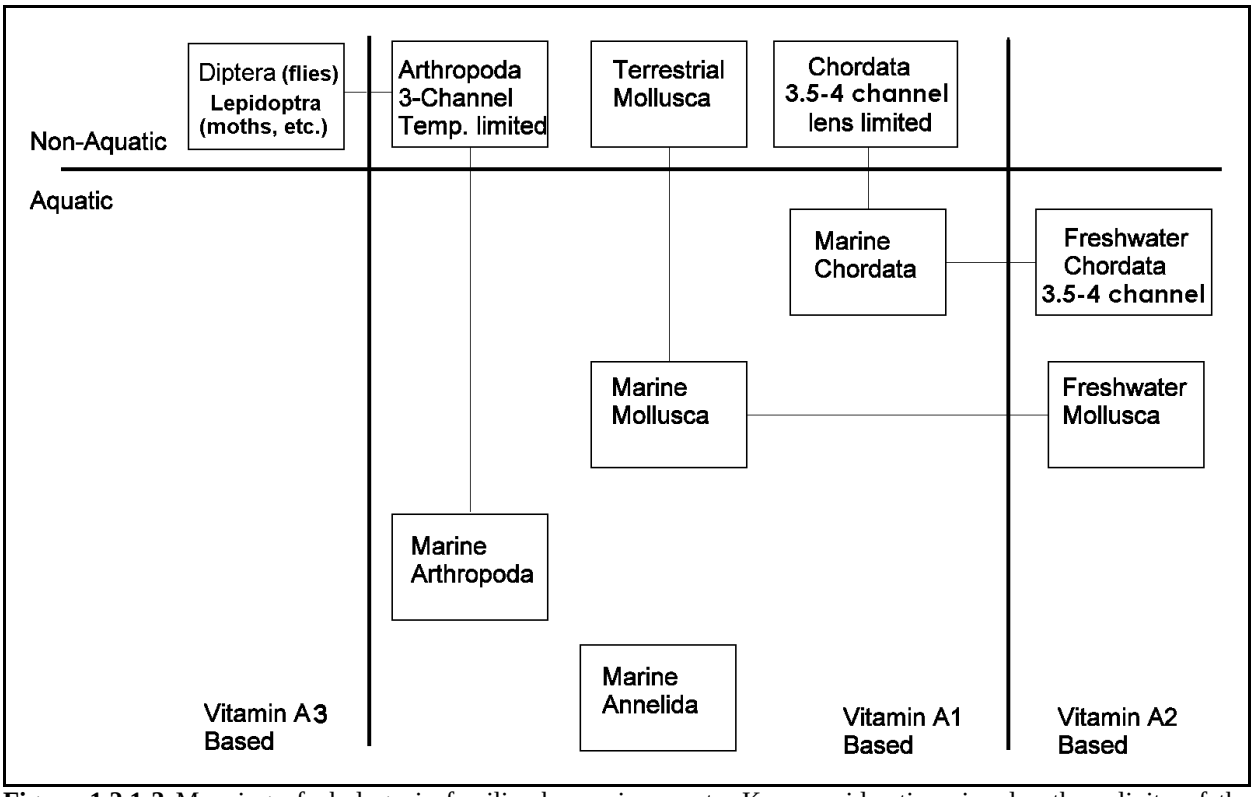

Figure 1.2.1-3 Mapping of phylogenic families by environment. Key considerations involve the salinity of the environment, the food supply and the index of refraction of the visual medium.

For a more extensive discussion of many eye configurations and many references, see the recent review by Land and Fernald[25] or that of Ali[26] Unfortunately, the terminology of Land and Fernald differs in a number of ways from this

[22]Torma, H. & Vahlquist, A. (1988) Identification of 3-dehydroretinol (vitamin A2) in mouse liver. *Biochim. Biophys. A.* vol. 961, pp 177-182
[23]Vogt, K. (1989) Op. Cit. pg 146
[24]Rodieck, R. (1998) the first steps in seeing. Sunderland, MA: Sinauer Associates, pg. 468
[25]Land, M. & Fernald, R. (1992) The evolution of eyes. Annu. Rev. Neurosci. Vol. 15, pp. 1-29
[26]Ali, M. (1982) Photoreception and vision in invertebrates. NY: Pleunum Press 773-778

work. They speak of the conventional division of eyes into groups and then define the simple eye as single chamber or camera like. Such a designation is usually associated with the Chordate or Mollusca eye rather than the "simple" eye of Arthropoda where the term has historically been used[27]. Land & Fernald also provide a gratuitous statement that conforms to the conventional wisdom regarding photodetection. They do deviate from this wisdom slightly by saying the chromophore of photodetection is a ligand, or prosthetic group, of an opsin and not the opsin itself. However, they then indicate "Covalently attached to the molecules is a highly conjugated molecule, the chromophore, which is one of a family of only four close relatives of Vitamin A." There is no discussion defining which four relatives they are speaking of, and they do not further define the spectral characteristics of the four chromophores. This work will introduce a family of four close relatives of Vitamin A that was not considered by these authors. Other significant differences exist in photoreceptor cytology and operation; however, the portion on optical forms is interesting. They follow a different taxonomic path than here but many similarities in viewpoint exist at the detailed level. Recognition of the fundamental difference between the direct and indirect retinas, as representative of the Mollusca and Chordata phyla, is one of them. This fundamental difference is why the classification Protostomia and Deuterostomia are not used herein. A more appropriate classification system gives equal weight to *Annelida, Arthropoda, Mollusca,* and *Chordata* as representing four basically different optical forms.

Figure 1.2.1-4, modified from Land & Nilsson, shows the organization in morphology of the eyes in the visual modality among major classes and species[28]. It differs from Land & Nilsson in recognizing that opsin does not play a role in the rhabdomeric photoreceptors. Opsin's main role is in the formation of the disks forming a substrate for deposition of the chromophores (photo pigments) in eyes utilizing ciliary photoreceptors. Land & Nilsson provided an unusually long caption below their figure that appears to be trying to establish a very small gene pool common to all of these visual modalities originating in the Precambrian period.

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[27] In short, the simple eye of Land & Fernald is defined as the complex eye here, with the term, simple eye reserved for one type of eye found in Arthropoda, the ocellus.

[28] Land, M. & Nilsson, D-E (2002) Animal Eyes. Oxford: Oxford University Press Page 12

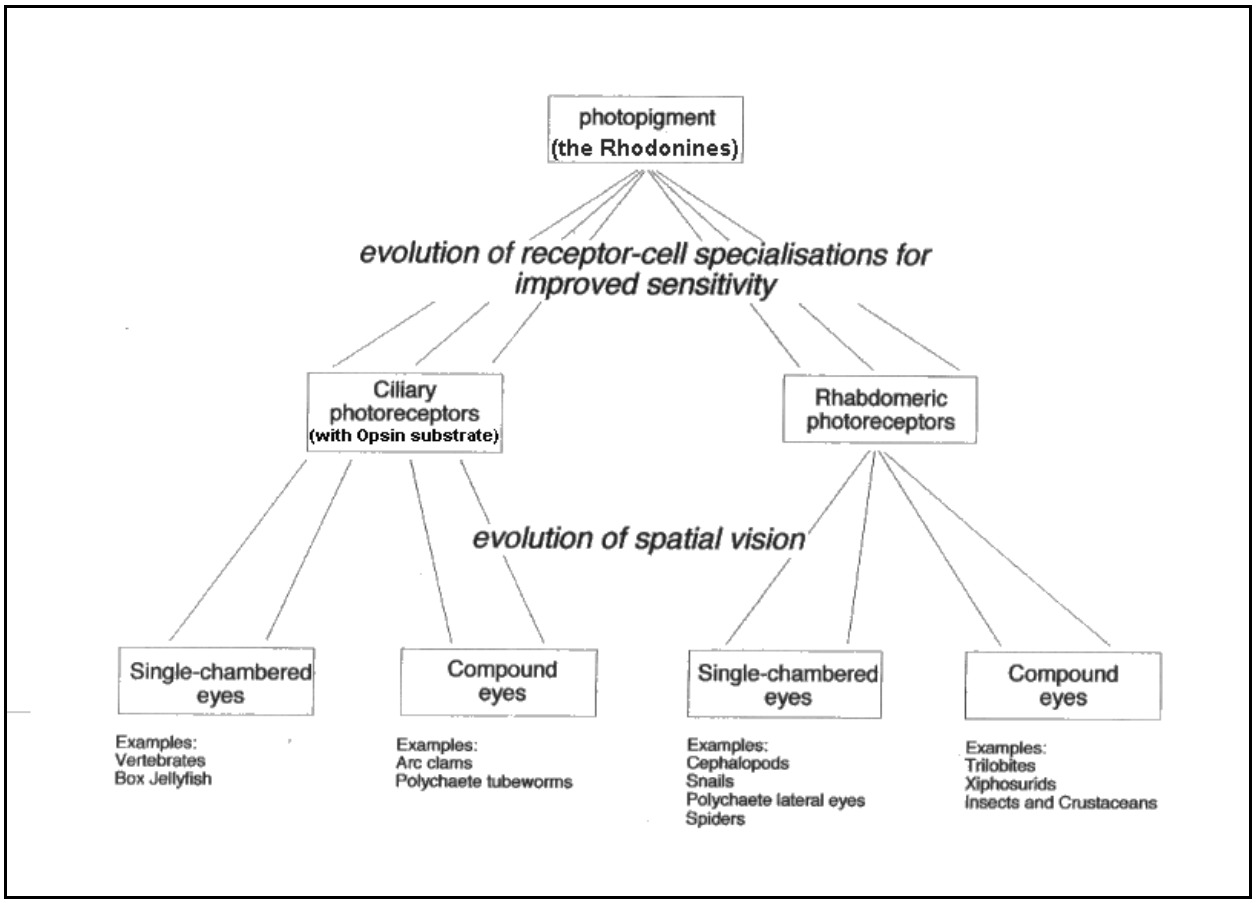

Figure 1.2.1-4 Different levels of homology among eyes. "All animal eyes share a homologous type of visual pigment but the various specialisations for accommodating large amount of visual pigment and for transducing the information into electrical signals appear not to be homologous" to the same degree. The protein substrate, opsin, has been separated from the non-protein diol photopigments (retinines) in the figure. See text. Modified from Land & Nilsson, 2002.

1.2.1.1.1 The ubiquity of ultraviolet vision in nature

Text books have yet to reflect a fact widely recognized in the research community. Tetrachormatic vision, involving four discrete chromatic photoreceptors, including one in the ultraviolet, is the baseline for vision in all of the major phyla of the animal kingdom. It is not a recent result of evolution. Studies purporting to trace the expansion of vision from monochromatic in "lower animals" to trichromatic performance in humans are largely spurious. Broad spectrum color vision dates from Paleozoic times (and humans are not the leaders in this area). Tetrachromatic vision has been widespread since at least the age of the insects. While various species exhibit more restricted spectral range for one reason or another, the typical animal is sensitive from the ultraviolet near 300 nm to the red beyond 700 nm. Various chromatic adaptation experiments have been carried out repeatedly that confirm that ultraviolet vision is associated with a distinct chromophore and is not merely an artifact of vision associated with one of the other chromophores. In Chapter 5, the UV chromophore is shown to be a natural member of the Rhodonine family of chromophores.

Two 1994 quotes from Bennett & Cuthill are particularly relevant[29]. "In short, UV vision appears to be found inmost animals." "Humans are atypical vertebrates in being UV-blind." Goldsmith highlighted this dichotomy in

[29]Bennett, A. & Cuthill, I. (1994) Ultraviolet vision in birds: what is its function *Vision Res* vol. 34, no. 11, pp 1471-1478

1991 by asking[30] , "why do very few animals, including man, ***not*** see in the UV?"

Issue 11 of the 1994 volume of Vision Research was devoted to ultraviolet vision in a wide range of animals. Bennett & Cuthill provided a long list of UV sensitive birds in their 1994 paper.

1.2.1.1.2 Environment and saline content are not criteria in taxonomy or vision

Parkyn & Hawryshyn have provided an interesting discussion of the salmonids[31]. Although exploratory rather than definitive in nature, their studies show the complexity in the taxonomy of this family. Taxonomy is itself a living science. Titles and designations change frequently on the scientific time scale. They stress that the species *Salmonidae Oncorhynchus mykiss* exists in two distinct forms, the anadromous steelhead trout and the freshwater coastal rainbow. trout. They also note that some species of salmonids travel back and forth repeatedly from the saline to the freshwater environment. They were unable to establish any difference in the spectral sensitivities of these species based on their environment at the spectral resolution of their experiments (20-nm windows). No difference in the retinas of these species was reported in their paper. This work suggests that any shift in spectral peaks of the functional chromophores of vision (those in both the liquid crystalline state and the resonant condition) due to the dominant variety of Vitamin A would be on the order of ±2-4 nm (**Section 6.2.2**).

1.2.1.1.3 Optimization at the Phylum level

Why each Phylum adopted a different visual system architecture cannot be answered in a limited space. Clearly, each of these Phyla adopted an overall system design which allowed it to exist, grow and evolve in its chosen sector of the environment. The characteristics of these system designs can be tabulated and listed in assorted orders to aid in this understanding. However, the ultimate design choices are not made by selecting from a dichotomy; the choice involves a weighing of all parameters. The type of visual system adopted is closely related to the mobility of the animal compared with other animals above it in the food chain. This mobility takes on two aspects, the ability of the animal to move quickly when required and its ability to augment its instantaneous field of view by motions of the structure supporting its eyes. Worms, which burrow into the soil, require only limited visual capability; their basic need is to know when they have reached the surface and are exposed to their most serious enemy, birds. Photospots are adequate for this purpose. Insects on the other hand live as a rule on the surface of the earth or on the surface of other plants and animals in a generally exposed condition. This leaves them continuously exposed to predators. To avoid being eaten, they have developed two prominent and fundamental capabilities. Although they generally move at a slow pace when foraging, they are capable of rapid escape maneuvers. To support this escape capability, they need good information concerning the presence of predators approaching from any direction. The compound eye is an excellent solution to this need.

> It is an interesting side note that military helicopters exhibit mobility characteristics similar to flying insects and have found a need for a similar threat sensing system. The insects, spending significant time on the ground, are usually equipped with sensors with hemispheric fields of view above the horizontal. The helicopter, spending significant time in proximity to the ground, is usually equipped with sensors with hemispheric fields of view both above and below the horizontal.

From this perspective, it appears that the simple eye (and possibly multiple simple eyes) has a different purpose. Because of the high mobility of many insects, they need a method of navigation. It appears the simple eyes support this need, particularly through their sensitivity to polarized light, frequently in the ultraviolet portion of the spectrum. Animals that maintain a generally slow unidirectional motion in a three-dimensional space frequently need nearly full spheric visual field of view to recognize predatory threats. Mollusca has achieved this capability through a variety of visual forms where the eyes are mounted to a fixed body element. They may use two eyes with very wide fields of view as in Squid and Shrimp, or a series of smaller eyes mounted along the periphery of a shell as in *Pecten*. Mollusca does not require eyes with high angular mobility and a complex eye with a direct retina is adequate for its needs. The need to cover a very large field of view at high resolution to sense threats at a range adequate for defensive, or offensive, purposes requires a large computational support facility. A solution to this problem is the use of a wide field sensing capability of nominal resolution augmented by a narrow field sensor of

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[30]Goldsmith, T. (1991) Optimization, constraint and history in the evolution of eyes. *Quar Rev Biol* vol. 65, pp 281-322

[31]Parkyn, D. & Hawryshyn, C. (2000) Spectral and ultraviolet-polarization sensitivity in juvenile salmonids: a comparative analysis using electrophysiology *J Exp Biol* vol. 203- pp 1173-1191

higher resolution. The narrow field sensor can be pointed at a detected threat or target to obtain more detailed information. This is the capability found in the more sophisticated members of the chordate Phylum. Although not immediately obvious, the inverse retina used in the chordate eye contributes significantly to the high angular mobility of the complex eye. It allows (forces) the grouping of the visual neurons into a concentrated bundle that is compatible with a high degree of rotary mobility. This angular mobility combined with the similar mobility provided to the head by the neck allows the use of a sophisticated "search while track" capability not unlike that used in modern military radars. Both systems make an allocation of the limited computational capability available between the two functions.

Based on the above limited discussion, there is a question whether the diphyletic theory of phylogeny is adequate. For purposes of vision research, considering a triphyletic theory based on a division into the Protostomic (Insecta), Deuterostomic (Chordata) and Tritostomic (Mollusca) branches (extended even to a Tetarstomic, or Annelida branch) might be more useful. The simpler solution may be to avoid the labels from the diphyletic theory, recognize the shortcomings of that theory and associate the different types of visual systems to the Phylum in which they occur. This is the course followed here.

An additional capability provided by both the direct and inverse forms of the complex eye is extremely important but virtually unrecognized. The basic sensing capability of biological vision is that of change detection. Without augmentation of the visual system, the animal is unable to perceive an image of a stationary or a very slowly moving scene. All frog hunters are aware of this situation. To achieve a satisfactory imaging capability, the higher animals in both the mollusc and chordate phyla use muscles to cause a small rapid oscillatory rotation of the eye ball. This capability will be discussed more thoroughly in **Chapter 7**.

Individual Families within a Phylum show additional optimizations of their visual systems to more effectively satisfy their needs within their niche environment. Optimization of this type has proceeded quite far. Even reaching the point where the visual systems used by different branches of one family may appear similar to those of another family in a different phylum, a process labeled conversion. Conversion is an example of two different species attempting to optimize their visual systems to meet the needs associated with a specific niche environment. The result is many special cases that are similar but in different phyla and many cases that appear bizarre until their reason for existing is discovered. This is particularly true concerning the optical systems. These can vary from an open pinhole in an otherwise closed chamber, to a multiple element system with a limited zoom capability. Some of these optimizations will be discussed at appropriate points below. Many of them involve modifications to the basic physiological optical system. Some are more sophisticated.

1.2.1.1.4 The place of *Planaria* and *Annelida*

Figure 1.2.1-5 shows a living *Planaria* and a cartoon of its visual apparatus. *Planaria* is a very early worm whose main feature is its bilateral symmetry. It is not a flat worm. It is not a segmented worm. It is a very primitive three-dimensional animal with a most primitive intestinal tract and without any skeleton. It is ubiquitous and found clinging to the underside of rocks in damp areas to this day. (A) illustrates its general plan form and the reason it is sometimes jokingly described as the cross-eyed worm. (B) shows the visual apparatus in more detail. It consists of two simple photosensitive systems; each consisting of a series of photoreceptor neurons arranged in a curve on the surface of the epidermis close to a generally curved ridge. The topology is extremely simple. Since the animal lives in a very two dimensional world on the underside of a rock, these two systems are adequate to indicate the direction to a changing source of illumination. The change may be in intensity but is more likely to be in position. Note carefully the two different illumination paths in the cartoon. In one path, the photoreceptor is illuminated at its distal end. In the second configuration, the photoreceptor is illuminated at its proximal end. The difference will be

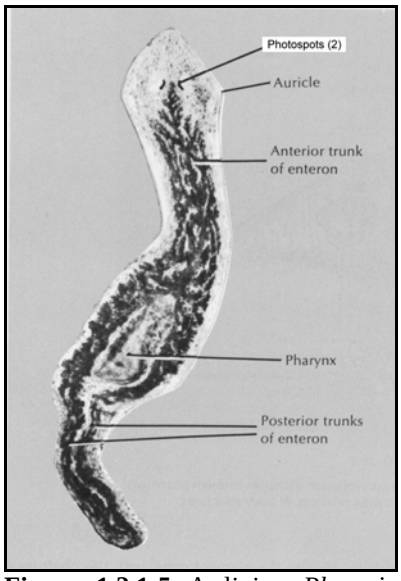

Figure 1.2.1-5 A living *Planaria* showing the two photospots (From Hickman, Fig. 13.2, 1979)

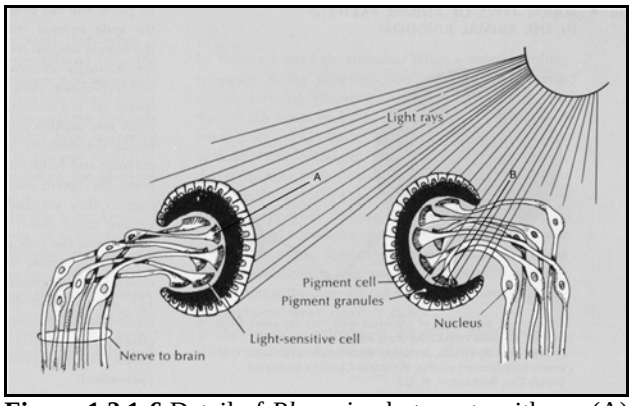

Figure 1.2.1-6 Detail of *Planaria* photospots with ray (A) illustrating the precursor of a direct photoreceptor retina and ray (B) showing how an inverse retina can evolve from the same structure. (Modified from Hickman, Fig. 13.9, 1979)

exploited by more advanced animals as discussed below.

Annelida follow the general visual architecture of the *Planaria* to this day. Other orders employ a series of more complex rules of topology to go beyond the simple visual structure of *planaria.* They create a variety of different eyes, all beginning from a slightly crenelated piece of epidermis with a sensing neuron exposed and lying on its surface. The photospots of *Annelida*, lacking an optical system, will not be defined as eyes in this work. Very limited data on vision in *Annelida* could be located[32].

1.2.1.2 Evolution of eyes

Various investigators have prepared artistic renditions describing different eyes found within the animal kingdom[33]. Many of these presentations are designed for introductory pedagogy and do not show the dual lens character of many eyes[34]. This work will take a narrower and hopefully more precise position concerning evolution in order to focus on the main trends. **Figure 1.2.1-7** shows a possible evolutionary path from the simple photospots of *Planaria* to the compound and complex eyes of the most advanced animals. Each of the different eyes is seen to evolve based on the replication of certain parts of the primitive photosensitive system. The top row contains two principal variants of the photospot that evolve into two major groups of eyes, those with direct and those with reverse retinas. The photospots do not form real images of the scene around them. The second row shows two primitive eyes. These eyes do not form images of the scene either. The third row shows the eyes of the more advanced visual systems. The two eyes on the right form obvious images of the external scene. The eye on the left also forms a cruder image relative to the total retina, the mosaic of retinulas, when the axes of the individual ommatidium are arranged to converge. The eyes to the left of the vertical line all involve direct retinas. The eyes on the right employ reverse retinas.

The direct photospots, can evolve in two distinct ways. First, a small group of seven to 25 individual photospots can group together with the epidermal layer surrounding them folding to the left in the figure in order to form a tube. Typically, the end of the tube becomes sealed by a transparent material that forms a lens. This lens focuses light on the small group of cells called a retinula. In the most common case, there are two refracting elements or lenses. The resulting assembly (A) is known as an ommatidium. It can also be described as a converse ommatidium to distinguish it from a similar assembly formed from a group of inverse photospots. The inverse photospots can form

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[32]Walther, J. (1966) Single cell responses from the primitive eyes of an annelid, *In* Bernard, C. *Ed*. The Functional Organization of the compound eye. NY: Pergamon Press pp 329-336

[33]Ali, M. (1982) Photoreception and Vision in Invertebrates. NY: Plenum Press. pg 776

[34]Gregory, R. (1998) Eye and Brain Oxford: Oxford University Press pg 26

an inverse ommatidium (not shown). In this case, the neurons would exit at the end of the photosensitive material nearest the lens group. The individual cells in the photosensitive assembly or retinula, are called rhabdom and generally form a circle of cells within the retinula. The external structure secreted by each of these cells is known as a rhabdomere.

The individual ommatidium can be considered the fundamental eye of the animal kingdom. The direct ommatidium can evolve into the three eyes of (B), (C), & (D) through different modes of replication. If the entire ommatidium is replicated, the compound eye of (B) results. It is the dominant eye in *Arthropoda*. If the second lens and the retinula are replicated behind but in close proximity to a single anterior lens, the structure known as an ocellus (B) results. This is a common configuration in both *Arthropoda* and *Mollusca*. If only the retinula is replicated behind a single anterior and posterior lens, the complex eye with a direct retina (D) results. This is the principal eye of the more advanced members of Mollusca.

By starting from an inverse photospot, forming a reverse ommatidium, and then replicating the retinula behind a two-lens group, the complex eye with a reverse retina (E) is obtained. This is the dominant, if not only extant, eye of Chordata. A recent text on the human eye has defined this eye as the simple eye of the vertebrates[35]. Having two eyes labeled simple is awkward. Further, the primary eye of *Chordata* is anything but simple. It is the most sophisticated visual system in existence. This work will confine the label simple eye to eyes found in invertebrate species. The same text has also provided caricature of a great number of conceptual variants of invertebrate eyes. The caricatures are based primarily on morphology and not functionality. Many do not conform to the accepted laws and terminology of optics. The group recognizes the difference between the terrestrial and aquatic environment but does not suggest the changing role of the cornea in these environments.

Both complex eyes of (D) and (E) exhibit an eyelid covering the optical path to the lens group of the eye. This structure is separate from the two-piece, bilateral, eyelid of *Chordata*. It is a separate single piece eyelid found in many species. When present in *Chordata*, it is frequently nictating and evolved into an auxiliary lens. It is rudimentary in humans. Complex eyes (D) and (E) also exhibit important mounting arrangements that are critical to their operation. These features will be discussed further in **Sections 1.2.1.4** and **1.7.3**.

[35]Oyster, C. (1999) The human eye. Sunderland, MA: Sinauer Associates, pp. 9-15

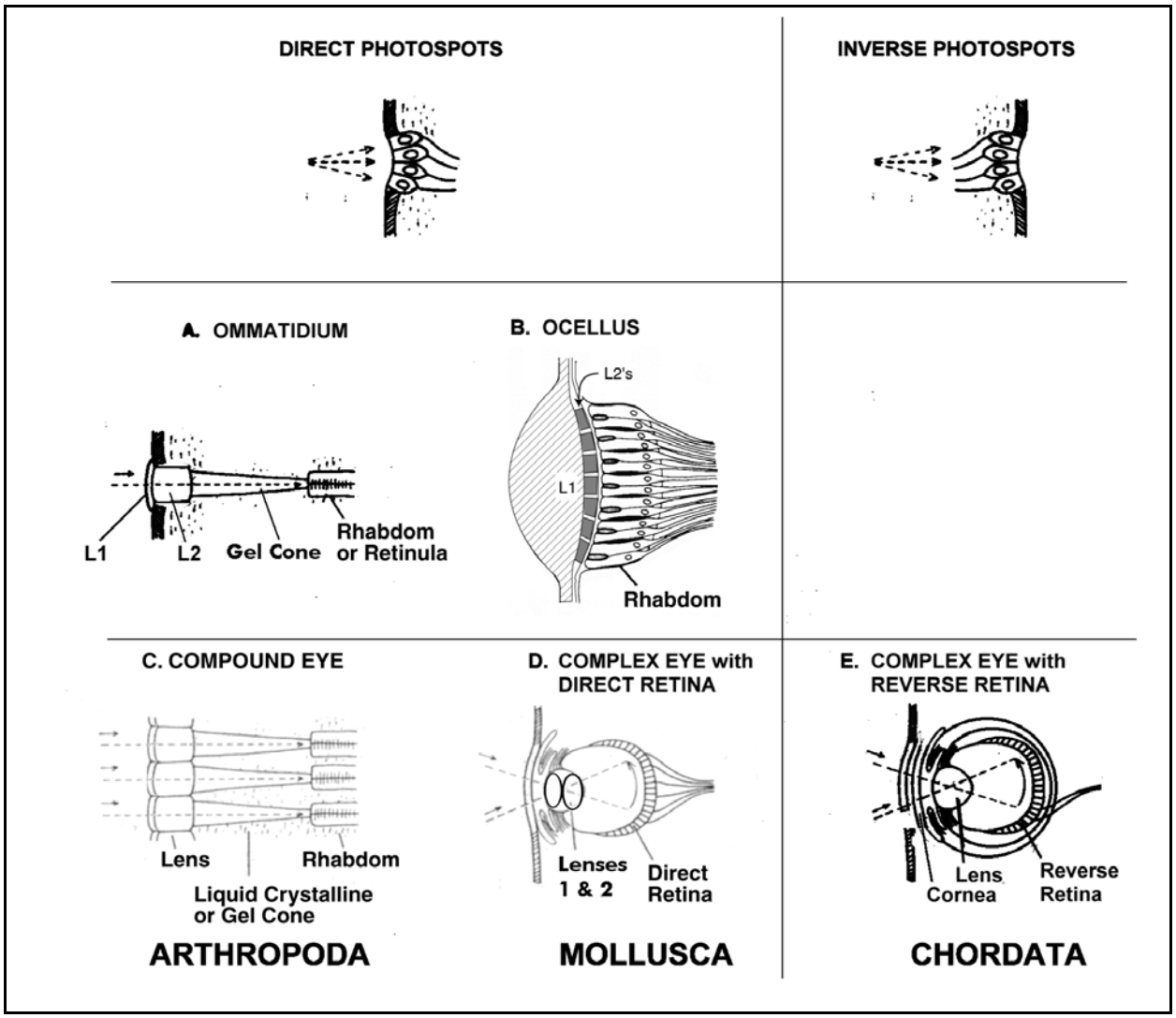

Figure 1.2.1-7 Evolution of the simple photospot into fundamental eye types by phylum. Top row; the direct and indirectly illuminated eye spots of the simplest bilateral animals. A; the fundamental ommatidium of *Arthropoda* showing the two lenses, the gel cone and the rhabdom. B; the ocellus or simple eye showing the rhabdom separated into its individual rhabdomin and rhabdomere (horizontal ellipses). C; the compound eye of *Arthropoda*, a replication of the ommatidium with the rhabdom forming a retina in the common plane of focus (not necessarily planar). D; the eye of *Mollusca* showing the directly illuminated retina body-mounted to the animal. E; the eye of *Chordata* showing the reverse illuminated retina mounted within a spherical eye ball able to rotate over a significant angle relative to the animal. The general plan is to have two distinct lenses in front of each type of retina, although the morphological names may vary. See text for details.

Although the complex eyes do not have the enclosed grouping of photoreceptor cells as seen in the retinula of the compound eye, there are repetitive patterns in the retina that hint at their heredity. Some of these patterns are quite distinct, particularly in *Mollusca* and immature *Chordata*.

1.2.1.2.1 Alternate photoreceptor irradiance

It is interesting that two different orientations of photoreceptors are possible in this evolutionary scenario. The first orientation has the distal end of the photoreceptor cells pointing toward the original epidermal ridge and resulting in the direct retina form of some *Arthropoda* and all *Mollusca*. The second orientation has the distal end of the photoreceptor cells pointing away from the original epidermal ridge and results in the inverse retina form of *Chordata*. Note that the method of epidermal enfolding is very important. In *Mollusca*, both the simple enfolding of

the *nautilus* and the more complex double enfoldings of the *loligo* (squid) are seen. In both cases, the eye is essentially hard mounted to the body by the large cross section of the combination of the optic nerve bundle and the blood supply. However, this hard mounting exhibits one degree of freedom as discussed in **Section 1.2.1.4**. In *Chordata*, both the simple enfolding and the double enfolding are possible but no eye employing simple enfolding has been reported. In Vertebrata, triple enfolding accompanied by the less extensive cross section of the bundle containing the optic nerve and blood supply allows for the formation of a freely rotating ocular. This provides a clearly superior eye for predators able to move quickly with a great deal of agility.

1.2.1.2.2 Alternative arrays of photoreceptors

Although it is common to think of the arthropod eye in terms of a multitude of unit elements based on the optical design of each unit, it is just as useful to look upon such eyes in terms of an array of photoreceptors that each have a lens in front of them. In this way, all but the simple ocellus exhibit a common characteristic, the photoreceptors are arranged in a simple planar array. **Figure 1.2.1-8** shows, in caricature, the common features as well as the major differences in the arrays of the animal retina. The individual arrays are not at the same scale. Outer segments of individual photoreceptors tend to be larger than 1 micron (except in the ultraviolet) because of the wavelength of the light to which they are sensitive. While these arrays are highly regular over short distances in all species, they tend toward swirl patterns over long distances in many species. This may be related to the fact that a tightly packed regular array of hexagons and/or squares cannot be used to form the interior of a spherical surface.

While the caricatures do not purport to define the chromatic performance of the individual photoreceptors, except in (c), All of the arrays are compatible with the tetrachromatic proposal of this work and some are compatible with the detection of the polarization of the incident light. The literature generally reports *Arthropoda* (a) sensitive to the three short-wavelength spectral channels, UV-, S- & M- and frequently exhibiting a sensitivity to polarization in the UV-channel. Although the data base is thin, *Mollusca* (b) is generally described as only sensitive to two wavelengths, M- & L- although recent experiments suggest S-, M- & L-. The performance of *Chordata* (c & d) is well documented. It generally shows sensitivity to either all four channels (the potential in most species) or, in the case of the larger chordates, only the longer wavelength triplet, S-, M- and L-.

The eye of *Arthropoda* **(a)** generally exhibits groups of seven to nine photoreceptors arranged very regularly in a loosely packed hexagonal array. The loose packing is compatible with the large area of each lens in front of each retinula. The example from Franceschini shows only seven photoreceptors arranged in a tight group as seen in the retina of a common fly[36]. The variations in the constituents of these groupings will be discussed below. The solid dots shown will be discussed in **Section 1.7.2.1**.

The eye of *Mollusca* **(b)** employs groups of photoreceptors that show many common attributes to those of *Arthropoda*. This example is from Octopus[37]. However, the individual photoreceptors show a bi-symmetry not shared with *Arthropoda*. This makes the groups of photoreceptors exhibit a regular square array instead of a hexagonal array. The square array also achieves a higher packing density than that of Arthropoda, since the Outer Segments of four or more photoreceptors can share the same optical footprint (providing a multilayer absorber similar to man made color photographic film).

The eye of Chordata also exhibits a very regular array of photoreceptors locally. The array shown in (c) is believed to show the morphological arrangement of photoreceptors in the tetrachromatic eye of the freshwater trout *Salmo trutta*[38]. The examples show the cross section within the Inner Segment region of the retina. The left part of the frame shows the observed photoreceptor array of a “yearling” trout. While no attempt was made to characterize the spectral performance of the photoreceptor at each location in the array, the fact that the two-year-old trout shown on the right did not exhibit ultraviolet sensitivity led Bowmaker & Kunz to the conclusion that the solid dots probably represented the ultraviolet photoreceptors. Bowmaker & Kunz characterized the spectral sensitivity of these animals and showed their peak sensitivity was compatible with that predicted by this work, 352, 437, 532 & 625 nm (although their spectrometer was limited to 370 nm).

The potential atrophy of the ultraviolet photoreceptors during early maturation is interesting when compared with the

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[36]Franceschini, N. (1985) Early processing of colour and motion in a mosaic visual system *Neurosci Res Supplements* vol 2, pp S17

[37]Young, J. (1971) The Anatomy of the Nervous System of *Octopus Vulgaris*. Oxford: Clarendon Press, Chap. 16

[38]Bowmaker, J. & Kunz, Y. (1987) Ultraviolet receptors, tetrachromatic colour vision and retinal mosaics in the brown trout, Salmo trutta; age-dependent changes. *Vision Res*. vol. 27, no. 12, pp 2102-2108

atrophy of many ganglion cells during early maturation noted even in humans[39]. However, such atrophication does not occur in humans (See **Section 17.2.4)**.

While the caricature of Bowmaker & Kunz stressed the square aspects of the photoreceptor packing arrangement, (d) shows the ease with which their arrangement can convert into a filled hexagonal packing arrangement during further maturation. This is the more common packing arrangement associated with retinas of *Chordata*.

1.2.1.2.3 Alternate photoreceptor configurations

A clear distinction is made in the literature between the arthropod and chordate type eyes. Their analogous parts are named differently. The chordate type exhibits chromophoric sacks that are disk shaped and the plane of the disks is perpendicular to the optical axis of the OS associated with the cell. The arthropod type exhibits chromophoric sacks that are cylindrically shaped and the axis of the cylinders is perpendicular to the optical axis of the ommatidia. Whereas the bulk of the photoreceptor cell lies along the side of the cylinder stack in *Arthropoda*, it lies at one end of the disk stack (the Outer Segment) in *Chordata.* Only fine structures (historically labeled microvilli) extend alongside the disk stack in *Chordata*.

The literature is less clear concerning the terminology to be used for mollusc type eyes. Inspection shows that the mollusc eye is not a simple replication of ommatidia but the labels from Arthropoda are frequently used because of the placement of Mollusca in the diphyletic taxonomy. By placing Mollusca in a separate wing of a phylogenic tree, it is possible to be more precise in the definition of components of the mollusc eye.

The literature frequently makes a distinction in the types of photosensitive structures in eyes according to whether the structures evolve from cillia or from microvilli--or involve laminar characteristics. These terms are not carefully defined in the literature to insure they are orthogonal to each other. This differentiation is also highly controversial.[40] As will be shown later, an alternate hypothesis for these structures is based on secretion instead of invagination. Therefore, this distinction based on cillia or microvilli is not supported in this work.

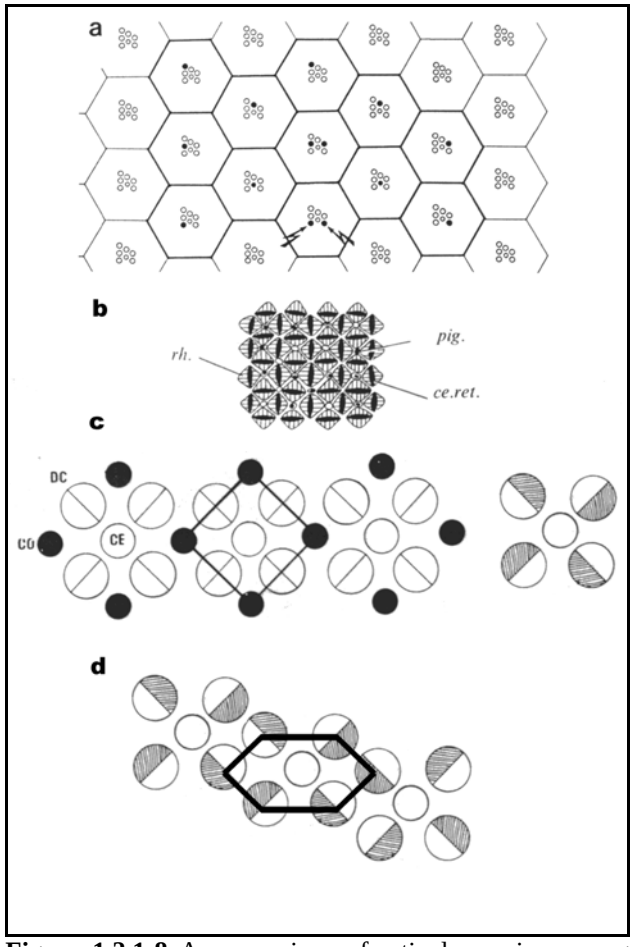

Figure 1.2.1-8 A comparison of retinal mosaics among phyla. A; shows the highly regular retinal array of a fly representing *Arthropoda.* Each retinula exhibits an identical grouping of photoreceptors. (From Franceschini, 1985). B; shows an array representing *Mollusca* with a rectangular arrangement. (from Young, 1971). C; shows the ordered array in the fresh water trout, *Salmo Trutta* representing *Chordata.* The tetrachromatic arrays of yearling trout are shown on the left. These arrays degenerated into trichromatic arrays by the second year as shown on the right. (From Bowmaker & Kunz, 1987). D; a modification of C to highlight the ease of moving to a hexagonal photoreceptor arrangement during maturation.

The compound eye, as historically defined, appears in several different phyla, as defined by the diphyletic theory. This situation may suggest the inadequacy of the diphyletic theory or it may suggest how much convergence that has occurred over time. Under this definition, there are two distinct types of compound eyes. Insecta generally associates a lens with each rhabdom; Mollusca generally exhibits a single lens serving many rhabdoms. If the phylogenic tree defined above is used, the overlap is reduced because the eye of Mollusca is defined as a complex

[39]Reh, T. (2001) *In* Ryan, S. *ed*. Retina, 3rd ed. St. Louis, MO: Mosby pg 17-18

[40]Autrum, H. (1981) Handbook of Sensory Physiology. NY: Springer-Verlag vol. VII/6B pp. 6-9

eye, instead of a compound eye. At the phylum level, all compound eyes are found in Arthropoda and all complex eyes (with a direct retina) are found in Mollusca. At the family level, there may be some exceptions such as one group of Annelida, the *Sabellid*-tube worms. It also leaves nearly all compound eyes with replicated optics and all complex eyes with a single optic. Further background can be found in Land.[41]

1.2.1.3 *Arthropoda*

Arthropoda has evolved two closely related visual systems, the simple eye and the compound eye. This work uses a narrow definition of a simple eye (See **Section 1.7.1.2.1**).The simple eye, corresponding to a single ommatidium (see **Section 1.6.2.1**), contains what is usually (and possibly inaccurately, see **Section 1.6.2.3**) called a dioptric assembly delivering light to a small group of photoreceptor cells called the retinula. Both assemblies are surrounded by an enclosure that may be optically opaque, either permanently or varying diurnally. This opaqueness may be due to a surrounding pigment or to total internal reflection. In some deep sea species, the envelope need not be opaque since there is so little stray light available.

A single ommatidium may be used alone as a simple eye (ocellus), used with other ocelli to achieve triangulation for navigation, or it may be replicated into a compound eye.

The compound eye of Arthropoda is a highly replicated structure of individual ommatidium as defined above. There are two ways to view this replication process. One can view the retinula as a sector of a larger two-dimensional retina with the optical elements formed in support of each retinula. Alternately, one can assume the replication of complete ommatidium in such a way that the retinulas are positioned to form a plane that can be defined as a larger retina.

While the compound eye is highly replicated, the overall geometry of the resulting package may vary immensely. To get a good overview of the variation in the compound eyes of *Arthropoda*, one need only visit the website of the Oklahoma Microscopy Society, www.uglybug.org.

The individual ommatidium has been described variously by a great number of investigators. In many cases, a tapered section behind a more easily labeled refractive lens is described as a light pipe. Such a light pipe involves reflection of light at its longitudinal surfaces. Where this designation is correct, the description of the optical system as dioptric is inappropriate since an optical system involving both refraction and reflection is catadioptric by definition.

There is a similar problem when defining a retinula. The form of the word would suggest a small but multi-element retina. However, particularly in the case of an optical system containing a light pipe, it appears all of the light from the optical system converges on a single pixel and the photoreceptor cells of the retinula all share this light. From an imaging perspective, this would suggest the cells behind a single optical system comprise a single elemental area of the larger retina of the compound eye. Such a grouping is usually described as a rhabdom. It may contain multiple individual photoreceptor cells.

Figure 1.2.1-9 provides more detail in a caricature representing a generic ommatidium of Arthropoda. There are so many different cartoons of an ommatidium in the literature that adding another one is not desirable. The variety is partly due to adaptation by different families to meet their environmental needs. It would be preferred to have a photograph of "the prototypical ommatidium." However, lacking a suitable picture, using a cartoon is necessary. (A) is a modified version of Stavenga & Hardie[42]. (B) is a modified cartoon from Smith, et. al.[43] providing a more detailed view of the retinula. In both cases, this simple eye consists of a light-sensitive assembly, the retinula or rhabdom, behind an optical assembly. The rhabdom is cylindrical in structure and contains an outer group of individual photoreceptor cells, ranging from five to 15 in number with their Outer Segments or rhabdomere forming an inner circular area. Some authors have defined the photoreceptor cell, less its rhabdomere as a rhabdomin.

Recently (2016), Chen et al. have provided a significantly different cartoon of the compound eye of a group of butterflies[44]. The paper describes an upper (R1-R4, distal receptors), lower (R5-R8, proximal receptors) and

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[41]Land, M. in Land, M. in Autrum, H. (1981) Handbook of Sensory Physiology. NY: Springer-Verlag vol. VII/6B pg. 543

[42]Stavenga, D. & Hardie, R. (1989) Facets of Vision. NY: Springer-Verlag pg. 360

[43]Smith, Stamnes, & Zucker, (1991)

[44]Chen, P-J. Awata, H. Matsushita, A. Yang, E-C. & Arikawa, K. (2016) Extreme Spectral Richness in the Eye of the Common Bluebottle Butterfly, Graphium sarpedon *Front Ecol Evol* vol 4, article 18 | http://dx.doi.org/10.3389/fevo.2016.00018

terminal (R9, basal receptor) group of individual photoreceptors within a single ommatidia of *Graphium sarpedon nipponum*. However, they use a different receptor numbering arrangement. They indicated the total length of the ommatidium was about 900 microns in the frontal portion of the eye, "where the retina is thickest." They identified three types of ommatidia based on histological dimensions rather than electrophysiological performance. Their depiction does not indicate the polarization sensitivity of the ommatidia although they do provide some data relating to polarization among the butterflies. See **Section 1.7.2.1.1**.

(C) illustrates an efficient packing structure used in some crustaceans lacking the axial rhabdomeres, RA & RB. This structure provides polarization sensitivity while achieving a high absorption cross-section. Assuming the cartoon represents the retinula accurately, it is interesting to contemplate the purpose of a single rhabdomere on the right front sharing interdigitated rhabdomere with two different rhabdomeres. Does this provide an additional degree of precision in polarization measurement?

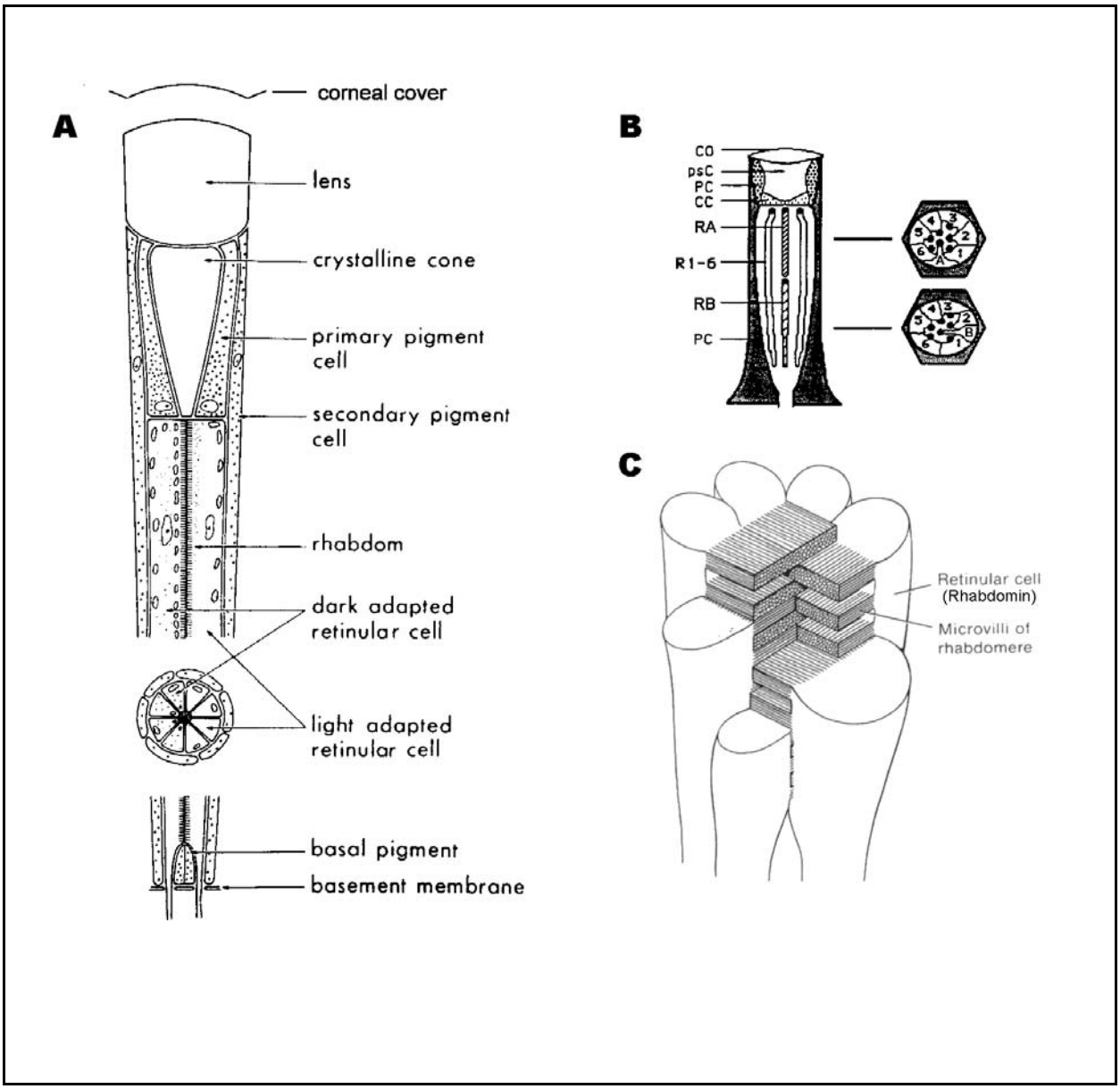

Figure 1.2.1-9 Generic ommatidium at two levels of detail. A; Ommatidium of a typical compound eye of the apposition type. From Stavenga & Kuiper, 1977. B; Ommatidium with less developed optics but more detailed rhabdom. Discrete rhabdomeres form an inner circle with two rhabdomeres, RA & RB, in tandem in the center of the circle. Rhabdomere RA is believed to be ultraviolet sensitive and connect through its rhabdomin directly to the optic lobe (medulla). RB may be blue sensitive. All eight Rhabdomin form an outer circle to complete the rhabdom. From Smith, Stamnes & Zucker, 1991. C; Interdigitated rhabdomere of Arthropoda lacking the central rhabdomere, RA & RB. Structure is particularly adapted to detecting the polarization of light. From Horridge, 1968.

1.2.1.3.1 The optics in *Arthropoda*

The title lens is used widely in the anatomical literature of *Arthropoda,* frequently with little attention to its definition in optics. As an example, it is frequently pointed out in the literature that the "crystalline cone" acts as a light pipe and is not truly crystalline. It is reasonably liquid and is probably best described as a gel or *liquid crystalline material*. In this sense, it corresponds to the vitreous humor of the chordate eye.

The optical assembly is quite complicated. As will be discussed in **Section 1.7.1**, it should generally be considered to consist of two refractive optical elements. A corneal cover may be present which constitutes a lens and contributes to the optical power of the overall assembly. In most insects, it is the interface between the air and the corneal fluid. Because of the difference in refractive index, the power of this optical element may be significant in terrestrial species when only mildly curved. Alternately, the outer lens or cornea may be vestigial in some aquatic species. There is what may be a conventional thick lens abutting a light pipe, the crystalline lens. The light pipe or waveguide delivers the light to the entrance of the retinula without forming an image. The sides of the light pipe appear curved in many cartoons. This is an indication that the wall is affecting the dispersion angle of the light bundle. The result is the delivery of the maximum amount of light with a minimum dispersion angle to the rhabdom. Varela & Wiitanen[45] provide a set of refraction indices for the elements of the ommatidium in the bee, with an index as high as 1.490 for the corneal cover.

1.2.1.3.2 Photodetection in *Arthropoda*

The rhabdomeres have a complex internal structure. Each rhabdomere corresponds to the outer segment of the photoreceptor cell in chordate eyes. As shown in (B), the retinula frequently includes what appear to be two rhabdomere in tandem along the axis of the retinula. The corresponding rhabdomins are located along the periphery like the other rhabdomins. In other adaptations, these cells are absent and the remaining rhabdomeres are interlaced to make maximum use of the available space. The tandem cells are best labeled RA (apical) and RB (basal) to avoid confusion with the sequentially numbered circumferential photoreceptor cells.

Fernandez-Moran[46] provides additional information concerning the rhabdomere-rhabdomin interface at the electron-micrograph level. Caution is recommended in analyzing these images because of apparent moire pattern interference in the image of some rhabdomere. Many authors attempt to group, or pair, the various rhabdomere (usually as a function of how many are present). The pairing is logical but varies between families. The caption of the micrograph in Davson implies the rods (microvilli perpendicular to the axis of the ommatidia) within a given rhabdomere are arranged *approximately* radially with respect to the center of the rhabdom. Similar presentations imply the sets of rods in pairs of rhabdomere are perpendicular to each other. Structural considerations would suggest the rods within a given rhabdomere are parallel to each other.

Light travels down the length of the retinula. The photon absorbing chromophores of the rhabdomere are contained in the light absorbing rods associated with each rhabdomere and equivalent to the disks in the chordate eye. These rods are spaced along the retinula to accomplish several objectives;

+ avoid causing a sudden change in the index of refraction at the entrance to the rhabdom that would cause significant reflection of the delivered energy

+ selectively absorb the radiation according to the type of chromophore they contain

+ selectively absorb the radiation according to its polarization if needed by the animal

+ maintain the photon energy within the optical core of the rhabdom by exhibiting an average index of refraction that is higher than the surrounding materials.

In some cartoons of ommatidium, a basal pigment is shown at the proximal end of the retinula. This material can act as an absorber of any non absorbed radiation. Alternately, the material could act as a reflector to cause the incident energy to retrace its path through the core of the retinula. This can enhance the quantum efficiency of the overall process. In this later case, the basal pigment would be operating in a mode similar to the tapetum of some complex eyes.

According to the analysis of Tomlinson[47], the number and location of the individual photoreceptor cells are under genetic control. Harris, et. al.[48] and Campos-Ortega et. al.[49] discuss aberrant *Drosophila* eyes that lack the R7

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[45]Varela, & Wiitanen, (1970) in The Eye. Vol. 6. Davson, H. ed. (1974) NY: Academic Press pg. 66

[46]Fernandez-Moran, H. (1958) in The Eye. Vol. 6. Davson, H. ed. (1974) NY: Academic Press pg. 43

[47]Tomlinson, A. (1988) Cellular interactions in the developing Drosophila eye. Development, vol. 104, pp. 183-193

[48]Harris, W. Stark, W. & Walker, J. (1976) Genetic dissection of the photoreceptor system in the compound eye of Drosophila melanogaster. J. Physiol. (Lond.) vol. 256, pp. 415-439

[49]Campos-Ortega,, J. Jurgens, G. & Hofbauer, A. (1979) Cell clones and pattern formation: studies on sevenless a mutant of Drosophila melanogaster Willhelm Roux' Arch. devl. Biol. vol. 186, pp. 27-50

photoreceptor that is sensitive to ultraviolet (*Drosophilas* normally have eight photoreceptor cells). Alternately, the *Limulus Polyphemus* normally lacks the photoreceptor in the R7 position and the R8 cell has lost its photosensitivity, expanded morphologically into the vacated space, and undertaken other functions. Surrounding the photoreceptor cells of the rhabdom are additional cells containing material that appears colored under the microscope and is generally labeled secondary and tertiary pigment cells. These cells may be analogous to the Retinal Pigment Epithelium of the chordate eye and provide the rhabdomere of the ommatidium with ready access to additional chromophoric material. Although the photoreceptor cell numbering system is convenient in ommatidia, it is not fixed across Arthropoda and the spectral absorption properties of photoreceptors with a given number may vary in different species. In the generic case, each photoreceptor has an axon emanating from the ommatidia and synapsing with a neural cell before reaching the brain.

The orientation of the chromophoric material restricted to the surface of the cylindrical sacks of each rhabdomere introduces a sensitivity to the polarization of the incident radiation. Indications are that some photoreceptor/rhabdomere elements are paired to achieve angular polarization sensitivity.

The stacking of the cylindrical sacks along an axis parallel to the optical axis while surrounded by a separate medium would be analogous with the waveguide action found in chordate eyes. In chordate eyes, the disks are stacked along the optical axis and the surrounding medium is of a different index of refraction. In both the chordate and arthropod eyes, the size of the sacks is not relevant to the absorption of the incident radiation. However, these structures play a major part in controlling the dielectric constant of the absorption material that in turn prevents the reflection of most of the incident radiation at the first surface of the stack.

1.2.1.3.3 Evolution within *Arthropoda*

The immense variety within *Arthropoda* has led to extreme diversity in eye configurations. Exploring this range here is impossible. Nilsson[50] has written on this subject. **Figure 1.2.1-10** shows a cartoon of two eyes that have deviated significantly from the generic eye of the phylum. Further investigation is needed in the case of *Ampelisca* **(a)** to decide whether this eye is a result of adaptation or mis-tabulation of a mollusc with a calcareous shell covering its mantle as a member of Arthropoda. Although Nilsson describes this as a single-lens compound eye in *Arthropoda*, this work would describe it as a conventional complex eye with a normal retina, as usually found in *Mollusca*. The caricature of the deep sea decapod **(b)** suggests it has lost all imaging capability in this eye. The optical assembly is largely missing and the rhabdom have expanded to fill the space available in an unspecified manner. Under this interpretation, the structure has lost all angular resolution capability and retrograded from an eye to a photospot.

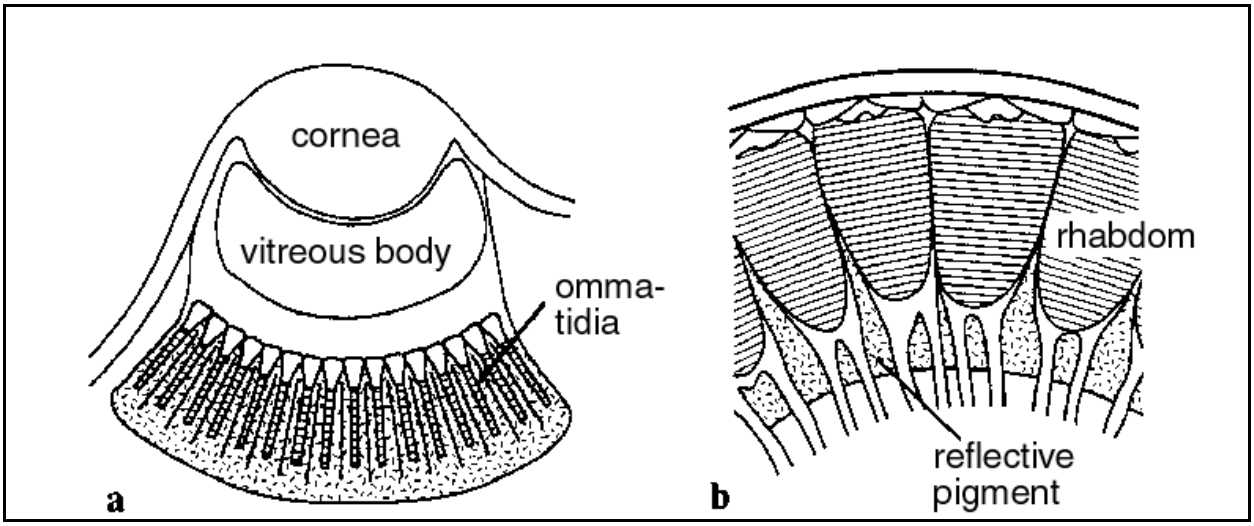

Figure 1.2.1-10 Modified compound eyes of two Arthropoda, Class *Crustacea*. a; The "single-lens compound eye" of *Ampelisca*. This structure approximates that of a nominal eye in Mollusca. b; Part of the compound eye of a deep sea decapod. The labels ommatidia and rhabdom do not conform to the nomenclature of this work. (From Nilsson, D-E. 1989)

[50]Nilsson, D-E, (1989) in Facets of Vision. Stavenga, D. & Hardie, R. eds. NY: Springer-Verlag. pp. 35-

A more important and unique adaptation is that found in the female marine copepod, *Copilia* of the class *Crustacea. Copilia quadrata* is found in the Mediterranean Sea and *Copilia mirabilis* is found in the Caribbean at depths of 200-300 meters[51]. **Figure 1.2.1-11** shows an eye employing physical scanning over a significant field angle. The Crustacea are bilateral and each animal has two of these eyes. The unique feature of this system is the use of mechanical scanning to achieve a significant field of view. Using the words of Wolken, each eye consists of an "expanded ommatidium" with significant space between the corneal, or anterior, lens and the posterior lens. The posterior lens is in conventional contact with the rhabdom. This combination structure is attached to a muscle that causes the structure to oscillate back and forth in the image plane of the corneal lens. As a result, the instantaneous field of view, of the single photoreceptor, is swept through an angle of as much as 14 degrees. The literature is excellent but partially contradictory[52, 53]. The dominant position is that the two sensory structures move in synchronism and opposite directions as if they were connected to the two ends of a single muscle. The scanning patterns, along one axis, are sawtooth in form and vary from one scan per 2 seconds to 5 scans per second. The literature is not specific as to whether any scanning occurs in the orthogonal direction, thereby forming a raster in the object field. Downing does provide a cross-section view showing the animal is cylindrical and that the "boomerang shaped element containing the rhabdom is not in the plane of the optical axes." It also shows the field of view of the optics at the focal location. At rest, the two optical axes are parallel. Therefore, there is little overlap in the scanned areas. The musculature could probably support raster scanning but the most detailed observations have been perpendicular to the plane of the two eyes. The space between the anterior and posterior lenses is reported to be of lower index of refraction that appears to be graded. The result is a telephoto optical system that is quite fast, *f*/1.6. This places the sensitivity of this eye in the class with fish. The overall arrangement is simple but inefficient in the use of available space. It also places a different type of data processing load on the brain. The bulk of the data is received in temporal sequence instead of in parallel as in most other animals. It has not garnered a significant place in the visual systems of animals.

Howard has summarized the reports of Land[54] and of Forster on the anterior median pair of eyes of the jumping spider, *Araneae Salticus*[55]. These are complex eyes. They exhibit significant performance based on a moving retina behind a single fixed lens. These retinas are finite in size and contribute to a significant imaging capability. The retinas exhibit at least three modes of conjugate movement in addition to a 50 degree rotation about the visual axes. Of equal interest is the quadruple layers of the retina, each with photoreceptors supporting a distinct spectral channel. Their arrangement appears to be in agreement with the chromatic aberration of the lens. The anterior median eyes provide a steerable high resolution multicolor image of a portion of the larger field of view associated with the anterior lateral eyes. The anterior lateral eyes exhibit a binocular region.

A mollusc has improved on this basic scheme of moving the retina behind a lens as noted in the next section.

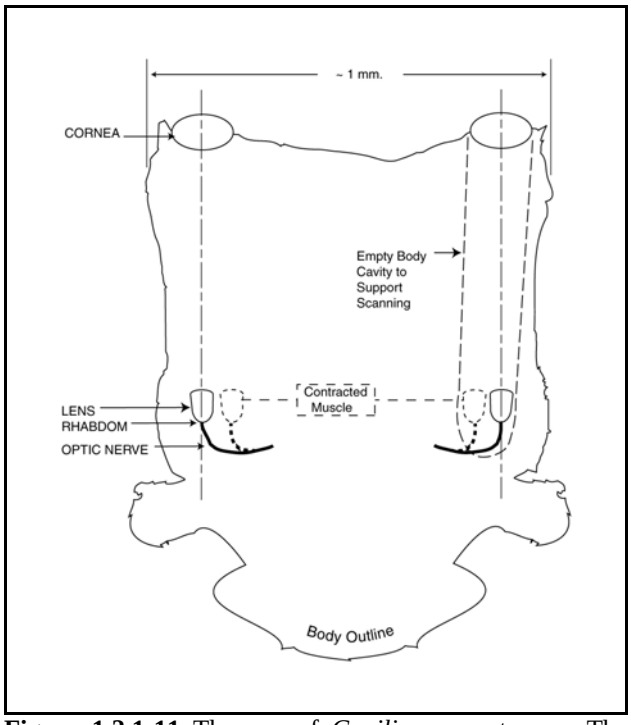

Figure 1.2.1-11 The eye of *Copilia*, a crustacean. The muscle is shown symbolically. Traced from Moray as presented in Wolken (1986)

1.2.1.4 *Mollusca*

Mollusca as a phylum offers at least as much variety among visual systems as *Arthropoda*. An interesting parallel with the point scanning arrangement of *Copilia* is the line scanning arrangement found in a few

[51]Wolken, J. (1986) Light and life processes. NY: Van Nostrand Reinhold pp. 142-145
[52]Moray, N. (1972) Visual mechanisms in the copepod, *Copilia*. Perception, vol. 1, pp. 193-207
[53]Downing, A. (1972) Optical scanning in the lateral eyes of the copepod, *Copilia*. Perception, vol. 1, pp.247-261
[54]Land, M. (1969) Movements of the retinae of jumping spiders (*salticicae: dendryphantinae*) in response to visual stimuli *J Exp Biol* vol. 51, pp 443-493
[55]Howard, I. (2002) Seeing in Depth, Volume I, Basic Mechanisms. Toronto, Canada: I Porteous, pp 535-536

heteropods[56]. *Pterotrachea coronata*, employs a long array of photoreceptors, roughly 6 receptors wide by some 410 receptors long. This line array is mounted behind an optical system in a spherical globe that is gimbaled along one axis. The eye is essentially external to the animal and rotates through about 100 degrees. As a result, the line-scan array sweeps out a field of about 100 degrees by 160 degrees. The eye rotates at about 250 degrees per second when sweeping downward and about 80 degrees per second. Assuming the higher number is similar to a retrace, the active scan at 80 degrees per second means a fixed point source in the field crosses one photoreceptor in approximately 14 ms.

Mollusca has also evolved a sophisticated eye form competitive with that found in *Chordata.* They both evolved what will be defined here as complex eyes, eyes with a single optical system and many photoreceptors assembled in a retina. In these cases, replication of the photoreceptor element occurred behind, and separately from, the single optical system. However, two fundamentally different approaches were employed. *Mollusca* formed the eye so that the incoming light encountered the end of the photoreceptor cell farthest, distal, from the nerve ending. The result is called a direct retina. The *Chordata* formed the eye by enfolding the tissue differently. It arranged for the light from the dioptric system to encounter the end of the photoreceptor cell nearest, proximal, to the nerve ending. The result is called an inverse retina.

The variety of eyes found in *Mollusca* is immense. Looking only within the Class Cephalopoda, there are hundreds of widely divergent species[57]. The Order *Nautilida* includes over a dozen species. The Order Teuthida contains the "squid" and includes over twenty families in two large sub-orders. The smaller specimens familiar to biology, (including the dwarf squid with the "giant" axon, *Loligo),* are in the sub-order *Myopsina*. The larger squid (including the "giant squid *Architeuthis*) are found in the sub-order *Oegopsina*.

Figure 1.2.1-12 is a cartoon of the eye of *Nautilus* that, although not typical, can be considered the prototype of mollusc eyes. The eye is body mounted, uses a direct retina and includes a rudimentary optical system, a pin hole, at the aperture of the enclosure (a "camera" in most romance languages). The cartoon would be more accurate if it showed a mucous film covering the pin hole and probably extending into it[58]. This mucous would help illustrate how the epidermis surrounding the pin hole could extend itself to cover the pin hole, or begin to extrude a protein substance instead of mucous to form a corneal layer covering the pin hole. A pin hole is a high *f*/# lens in optical terminology. It is poor in light collecting ability but is excellent in aberration control. In most, eyes, better light collection is more important than aberration control and a more sophisticated lens system has evolved. Therefore, the generic eye of *Mollusca* will be considered an eye as in Nautilus with the addition of a more sophisticated, although still simple, optical system

There is only limited material available concerning the histology of the mollusc retina and very little concerning the electrophysiology. **Figure 1.2.1-12** provides a typical cartoon adapted from Hickman. The element labeled optic ganglion is labeled the optic lobe in Young and he defines the optic nerve as connecting the optic lobe and the remainder of the brain. Most of all mollusc eyes employ a replicated assembly of retinula, the ommatidia without its optical assembly, behind a single optical assembly. Thus, the individual photosensitive assemblies of the mollusc eye, the retinula, appear very similar to that in the ommatidia of the Arthropoda on first examination. However, significant differences are seen:

[56]Land, M. (1982) Scanning eye movements in a heteropod mollusc. J. Exp. Biol., vol. 96, pp. 427-430
[57]Smithsonian Institution (2001) www.mnh.si.edu/cephs/newclass.pdf
[58]Muntz, W. (1987) A possible function of the iris groove of nautilus. In Nautilus. Saunders, W. & Landman, N. Ed. NY: Plenum Press. pp. 245-247

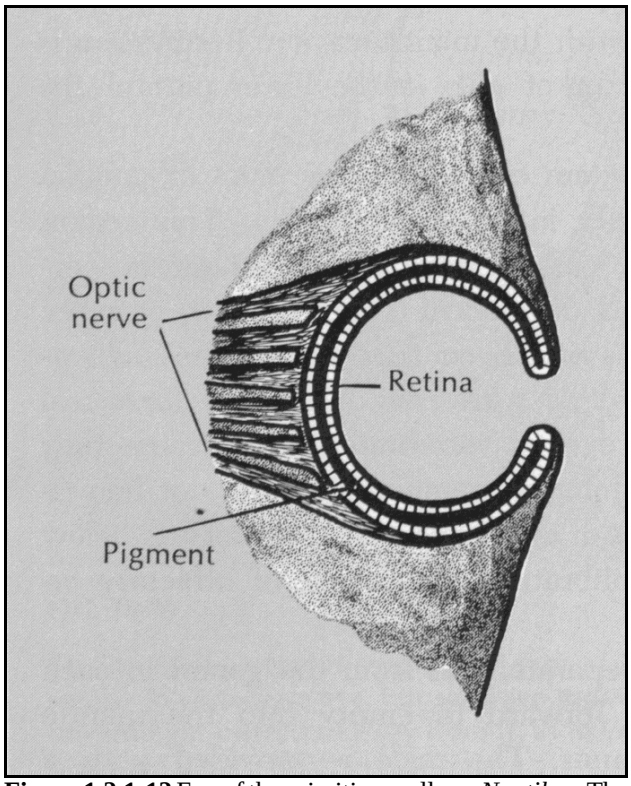

Figure 1.2.1-12 Eye of the primitive mollusc, *Nautilus*. The most well known pin-hole camera in the Animal kingdom. From Hickman (1970)

+ individual rhabdomins are frequently reported to exhibit two opposing sets of rhabdomeres.

+ the rhabdom in Mollusca often omits the axially located rhabdomere frequently found in the rhabdom of Arthropoda. The surrounding rhabdomeres frequently expand to use this space and frequently interdigitate to provide polarization information about the same region of the object scene.

+ the spectral channel associated with each rhabdomere may be paired with rhabdomere in different relative locations within the rhabdom than is typical in Arthropoda.

Based on observational studies, it is quite likely that at least the Cephalopods of *Mollusca* have photospots or simple eyes that help coordinate their ability to change skin color. To be effective, they must be multi-spectral. These structures may be located near the periphery of their bodies.

1.2.1.4.1 Evolution within the phylum

Evolution has progressed quite far in Mollusca. Although this Phylum consists of an immense number of species, and a large variety of eye morphologies, only the eyes of a very few (less than a dozen) have been explored in detail. Although the eye of *Pecten* and other unique forms occupy a significant position in the literature of the Mollusca eye, this is because of their speciality and not due to their typical characteristics. Because of its unique optical system, *Pecten* will be discussed more fully in **Section 1.7.1.3.**

One of the most interesting cases of physical adaptation is the eye of *Loligo*, the dwarf squid, shown in **Figure 1.2.1-13**. Although it is clearly a complex eye with a direct retina, it has evolved to the point where it may perform like a chordate eye in terms of an imaging capability. Note the near complete isolation of the eye from the body of the animal and the gap at the top of the cornea.

The morphological literature has assigned the name cornea to an outer structure in *Mollusca* that would be called a nictating lens in a *Chordata*. A nictating lens is actually a transparent second eyelid. Note the fact that this outer structure is not attached at both extremes and it is structurally independent of the eyeball. It does not conform morphologically to the conventional cornea. Note also how the outer cover has evolved easily from the situation in *Nautilus*. Recent studies have also shown the ability of this outer covering to move about within the optical path, apparently to form a variable shape pupil. Note the vertical line through the middle of the lens. This suggests two optical elements, the inner being the conventional lens and the outer being the cornea. A similar situation, with respect to both the outer covering and the two part lens is shown in Barlow, based on Wells and Kaestner[59]. It is proposed that the morphological terminology used to describe the visual system in the advanced cephalopods be modified to recognize the familial relationship of these features.

Although the eye still appears to be mounted to the body by significant structure, it can pivot about a point near the Optic Lobe of the brain. This mounting provides *one degree of angular freedom* (although small) and allows the eye to vibrate through a small

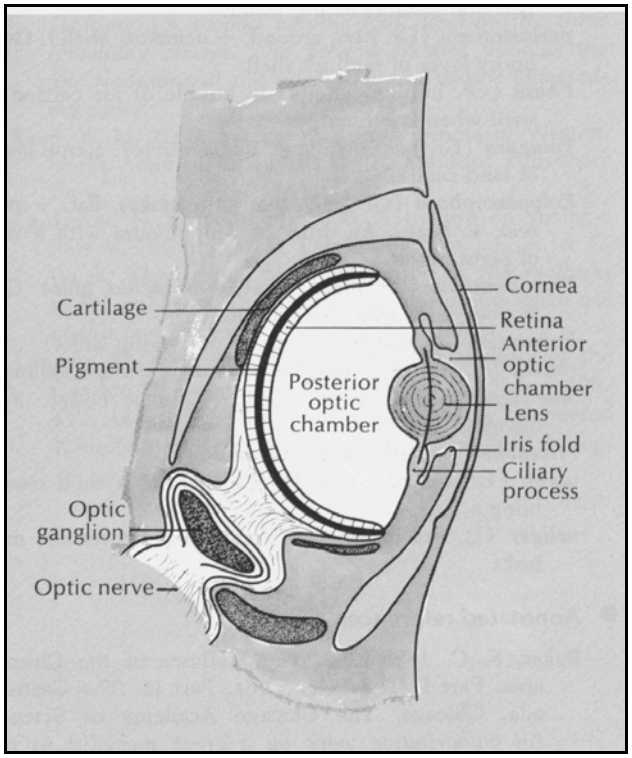

Figure 1.2.1-13 The complex eye of the dwarf squid, *Loligo*, showing its near separation from the surrounding tissue in order to achieve imaging through vibration around a pivot point near the Optic ganglion. More recently the optic ganglion has been labeled the optic lobe of the brain See text for proposed changes in morphological labels. (From Hickman 1970)

[59]Barnes, R. Calow, P. & Olive, P. (1988) The Invertebrates. Oxford: Blackwell Scientific Publ. pg 169

angle behind the cornea, achieving an imaging capability similar to the chordate eye without employing rotation. The notation in the picture is not consistent with a correlated description of eyes or the morphology of the neurons within the "optic ganglion." The label optic ganglion was probably assigned during early morphological studies. The structure is actually the optic lobe[60] of the brain and the structure labeled the optic nerve is actually a commissure, or intra-brain nerve bundle. The optic nerve is between the optic lobe and the eye. The optic lobe contains a variety of lateral and bipolar cells similar to the retina of the chordates. However, it does not contain neurons of the type associated with the reception of action potentials related to projection neurons. The optic nerve is not reported to contain projection neurons. It is therefore important that the eye be as close to the brain as possible to satisfy signaling requirements. The lack of projection neurons, and the consequent lack of action potentials, has probably impeded the electrophysiological study of the squid eye. This has resulted in some unusual conclusions drawn from psychophysical experiments concerning the color vision of octopuses.

The structure labeled cartilage actually plays the same role as the bone of the eye socket in advanced chordates. It is proposed that there is a small amount of muscle between this cartilage and the eye itself, similar to but less complex than in the chordate eye. Young[61] discusses the details of this muscle tissue based on the earlier work of Alexandrowicz (1927) By contracting repeatedly, this muscle provides the tremor needed for imaging purposes. While the above figure does not illustrate the pivotal capability of the eye, **Figure 1.2.1-14** does. This figure illustrates two points. There is a definite symmetry of the eye supporting a limited degree of rotation relative to one axis. This axis is found at the crossover point where the neurons traveling between the retina and brain create a chiasm. It also illustrates the woven nature of the optical neurons in their path between the retina and the optic lobe. This pattern insures that the neurons located along the "strip" of the retina corresponding to the fovea in chordate eyes, exhibit the shortest signal path between the eye and the brain. These features are also shown in Barnes, et. al. The caricature representing the lenses and aperture of this eye will be discussed in **Section 1.7.1.3**.

1.2.1.4.2 The putative eye of the "Giant Squid"

A "giant squid" has long appeared in mythology, and various large squid have occasionally washed up onto various beaches. Linnaeus refused to include a giant squid in his definitive taxonomy of animals (and it remained missing from his tenth edition). However, Wood does provide it a home and complete taxonomic designation on the current website, www.thecephalopodpage.org .

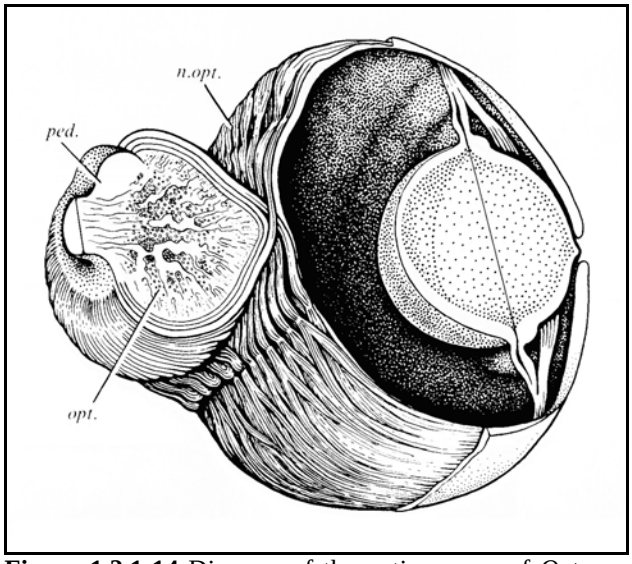

Figure 1.2.1-14 Diagram of the optic nerves of *Octopus vulgaris*. Note the axis, convergent with the chiasm in the optic nerves, providing a limited degree of rotational freedom. *n. opt.* are the optic nerves. *opt.* Is the optic lobe of the brain. *ped.* Is the peduncle region of the optic lobe. This author will take exception to the treatment of the lenses and aperture in this caricature. From Young (1971)

It is difficult to discuss the mythical eye of the giant squid without a drawing. Popular mythology dating from at least the 15th Century has it that the giant squid, being an inhabitant of the deep ocean has an eye the size of a dinner plate. This size is described as required in order to operate in the extremely low light level at these depths. Apparently, it is assumed that the sensitivity of the eye is determined primarily by the diameter of the lens and aperture instead of the normal criteria that it is determined by the *ratio* of the diameter of the aperture to the focal length. These are the parameters that determine the "luminance" falling on the retina. The size of the aperture only becomes important if the size of the individual photoreceptors were increased proportionately. Hughes has provided a graph of body weight versus aperture size of the eyes for a large range of [62]animals. This graph would suggest that the diameter of the eye of the putative giant squid is probably near 60 mm. The eye can be expected to

[60]Young, J. (1971) The anatomy of the nervous system of Octopus Vulgaris London: Oxford University Press. pg. 448

[61]Young, J. (1971) Op. Cit. pp. 420

[62]Hughes, (1977) The topography of vision in mammals of contrasting life style. *In*, Handbook of Sensory Physiology, Vol. VII/5 Crescitelli, F. ed. Berlin: Springer-Verlag pp. 613-756 *also in* Oyster, C. (1999) The Human Eye. Sunderland, MA: Sinauer Assoc. pg 17

operate at a very fast F/# similar to other deep water animals, probably F/1.0 to F1.5.

It is interesting to note the reference to the eye in a recent writing of Young[63] where he said: "in *architeuthis*, the giant squid, they are as big as car headlamps."

> Lacking any numerical precision in the above references, it is fortunate to note the reduction in the size of the eyes of *architeuthis* as the size of car headlamps have declined. In the year 2000, some headlamps were under seventy-five mm in diameter. In 2009, many more headlights are in the seventy five mm diameter class.

Ellis reiterated the primary fact in 2005 as part of a summary of the folklore of *architeuthis*[64]. "No one has ever seen a healthy adult giant squid–especially in its native habitat–but we assume they live at great depth." It is likely the eye of any existing giant squid has considerable decoration surrounding its true eye, as in the case of the reef squid, that makes the eye appear larger to one unaccustomed to this geometry. While Ellis includes a sketch of the giant squid and provides dimensions recalculated from 19th Century units, no photographic image of the eye of a giant squid, especially one including a unit of measure, could be found in the literature. The undetailed eye in the Ellis sketch appears to be about 150 mm in diameter.

It is also interesting to consider the proposition that whales hunt and eat giant squid, presumably in their natural environment. This might suggest that the eye of the whale (a maximum pupil on the order of 60 mm diameter (much smaller than that of the putative giant squid) is adequate for operation in the illumination environment of the giant squid.

> This argument is probably superfluous since the toothed whales undoubtedly uses its biosonar capability to catch *architeuthis* in the dark.

Recently, a very large and complete squid was brought to shore. While not 10 meters long, it was approximately 5 meters long and weighed ~1000 pounds. It was described as the colossal squid, *Mesonychoteuthis hamiltoni*. The eye ball had an external diameter of 270 mm (10.5 inches). We now know that many of the large marine animals have eyes where the active eye volume, defined by the choroid, is much smaller than the external appearance would suggest. The lenses of the eye of this *Mesonychoteuthis hamiltoni* are currently being studied. They are spherical with a diameter on the order of 80-90 mm range based on the video released during the early studies. Three specimens are currently on exhibit at the Museum of New Zealand Te Papa Tongarewa, http://squid.tepapa.govt.nz/ . An academic study has been published[65]. It indicated an optical speed for these eyes between *f*/2.5 and *f*/3.0 and a dependence on bioluminescence for detection of whales preying on the squid.

In 2013, the Discovery Channel Studios LLC produced a program where the diameter of the largest squid pupil was described anecdotally as 3.5 inches (99 mm) in diameter[66]. This number is compatible with and may refer to the squid now in the above museum. The joint Japanese/American team failed to land a giant squid but may have recorded imagery from one of unknown age and size. The length of the squid sans tentacles was estimated at 10-11 feet (3-3.3 m).

1.2.1.4.3 The neural system of the squid

The recent compendium by abbott, et. al. has provided a broad review of the neurobiology of the squid, octopus and cuttlefish[67]. Chapter 26 provides the architecture of the overall visual system, and its relationship to the central nervous system, CNS, of the octopus. Chapter 17 describes the major motor neurons of the squid controlling the escape reflex. Chapter 29 provides some morphological details concerning the retina of squid but the discussion related to the chromophores is not supported by this work.

1.2.1.5 *Chordata*

Currently, the first chordate is considered to be Pikaia, *Pikaia, gracilens*. Very little is known about this animal. It is

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[63]Young, J. (1991) Light has many meanings for cephalopods, Visual Neuroscience, vol. 7, pp. 1-12
[64]Ellis, R. (2005) Singing Whales and Flying Squid: The Discovery of Marine Life. Guilford, Conn. The Lyons Press pg 144
[65]Nilsson, D-E. & Warrant, E. et al. (2012) A Unique Advantage for Giant Eyes in Giant Squid *Cur Biol* vol 22, pp 683–688 DOI 10.1016/j.cub.2012.02.031
[66]Discovery Studios, LLC (2013) Monster Squid: The Giant is Real. http://curiosity.com/season2
[67]Abbott, N. Williamson, R. & Maddock, L. *ed*. (1995) Cephalopod Neurobiology NY: Oxford University Press

difficult to distinguish it from the earlier bilateral animals such as Planaria and the early members of Annelida. What little that is known suggests it probably had photospots similar to Planaria.

The archeological record of the eyes of *Chordata* is very limited; it does not show the wide variety of *Arthropoda* and *Mollusca*. Although it is logical to assume that a chordate with a pinhole eye like the current but ancient *Nautilus* once existed, no reference to such an eye could be found in the literature. It appears the current form found in nearly all vertebrates was developed early, found more than adequate, and continues in use to this day.

As will be explored more fully later, the ability of the chordate (which includes the vertebrate) eye to rotate in its socket is of crucial importance--from two different perspectives:

+ The ability of the vertebrate eye to oscillate at about 80 Hertz at a peak amplitude of about 40 arc seconds leads to its operation as an imaging sensor. (Without this oscillation, the vertebrate eye is a change detector and not an imaging device.)

+ In the highest vertebrates, the ability of the eye to achieve wide angular changes in fixation provides a much higher degree of situational awareness.

Figure 1.2.1-15 provides details of the anatomy of the human eye as representative of the phylum *chordata.* It includes three modifications from the original[68]. The conjunctiva is structurally different from the corneal epithelium. The call-out corneal epithelium has been added to stress this difference. Oyster[69] provides the details supporting this proposition. The second modification concerns the orientation of the Outer Segments within the retina. Originally, all of the Outer Segments were shown pointing toward a nodal point within the eye. This is incorrect. All fully functional photoreceptor cells point toward a point within the aperture of the lens (the 2nd principle point). They would point toward the center of the iris except for the bending of the central ray by the highly elliptical lens. Finally, this eye only exhibits one bilateral eyelid. A great many chordates possess two eyelids. The second being a nictating eyelid that consists of only a single membrane. When extended, this eyelid completely covers the cornea.

The third modification is to illustrate the very limited angular field of maximum spatial resolution and depth perception in humans. Stereopsis, or precision depth perception, is only achieved within this area (**Section 7.4.4**). The precision of depth perception falls by over two orders of magnitude outside of the 1.2 degree field shown Spatial resolution also decreases precipitously outside of this region (**Section 2.4**).

A further correction regards the cornea. The cornea is not of uniform thickness. The inner radius is shorter than the outer radius. This causes the cornea to be thinner on-axis than at its edge. This makes the cornea a negative meniscus lens, a key feature of all wide angle optical systems.

Unfortunately, the figure fails to suggest how the eye actually works. Without including the details of signal processing in both the retina and the rest of the brain as well as the motor-neuron system, understanding the operation of the eye is hindered considerably. What is initially sensed and eventually perceived by the animal is much more complicated than the notion of taking a picture.

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[68]Feduccia, A. & McCrady, E. (1991) Torrey's Morphogenesis of the Vertebrates, 5th ed. NY: John Wiley & Sons

[69]Oyster, C. (1999) The human eye: structure and function. Sunderland, MA: Sinauer Associates, pg. 352

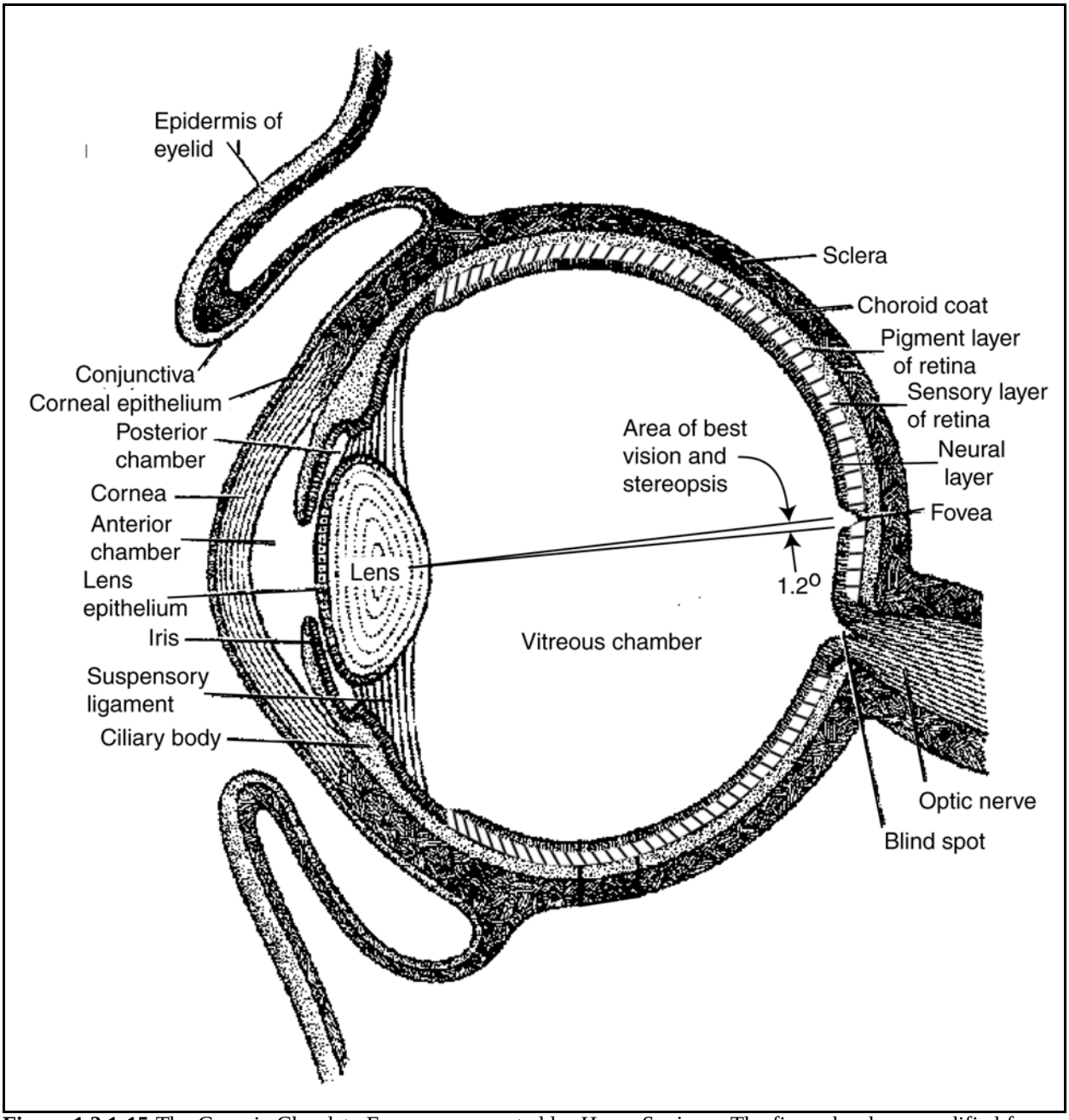

Figure 1.2.1-15 The Generic Chordate Eye as represented by *Homo Sapiens*. The figure has been modified from a similar earlier one. The corneal epithelium has been separated from the conjunctiva. The photoreceptors of the sensory layer of retina (coarse hatched lines)are pointing toward the center of the lens, not the so-called nodal point of elementary (small field angle and thin lens) optics or the center of the eyeball. The small area of maximum resolution and depth perception (stereopsis) is also shown. This 1.2 degree diameter area is associated with the center of the fovea, the foveola. Modified from Torrey's (1991).

As an example, the process of blinking the eye is closely coupled to the data processing function of "clearing the visual memory." Furthermore, many illusions and distortions are dependent on the rate of rotation of the eye in its socket. The operation of the eye muscles is generally predicated on the idea that very few significant events in

nature can occur in less time than it takes the eye to establish a new line of sight. Therefore the brain commands the eye to a new line of sight, the command is carried out in an open loop manner from a servomechanism point of view, and the brain assumes the new line of sight is established instantaneously. This assumption gives the magician and some other natural or man-made phenomena a grand opportunity to deceive the eye-brain system.

Another example is the second order signal processing within the retina. Many authors imply that the human eye is the most sophisticated in the animal kingdom. However, it is generally recognized that the frog eye involves a much larger amount of data processing in the retina than the human eye and can thus do things the human eye cannot. Whereas if something moves in the peripheral field of the human eye, a threshold is exceeded and the eye is commanded to bring its point of fixation to the approximate direction of the event. The peripheral retina of the frog eye however proceeds to calculate a trajectory for the moving event, and also to determine its probable identity, without causing a rotation of the fixation point. This saves valuable time in the food acquisition process.

The schematic shows four photoreceptor channels providing four different chromatic signals. This may appear as a surprise since the human has a strong tendency to think of itself as the most highly developed, most learned, most politically savvy, etc. In the visual arena, the human is definitely not supreme. A broad range of creatures has superior visual capabilities from one point of view or another.

1.2.1.5.1 Evolution within the phylum

Evolution at the family level has been very significant in Chordata, with many attempts to achieve new capabilities and occasionally converge toward capabilities found in other Phyla. The capability of meeting the basic wide angle search for threats has been maintained (usually using the information from several sensor systems) and several steps have been taken to improve the capability to track prey. Although Chordata includes many animals with eyes that do not have an overlapping field of view, this capability has been adopted in the more aggressive members of the phylum. Overlapping fields of view has improved the tracking capability of the animal in its primary direction of travel at the expense of a search capability in the opposite direction, to his rear. In the higher vertebrates, the problem of sensing areas to the rear has been alleviated by the presence of a neck, which allows for extending the field of view on an intermittent basis. Pointable external ears have also supported surveillance to the rear.

Full exploitation of the overlapping fields of view has placed a heavier load on the signal processing capability of the animal in order to extract stereo information. Another innovation in Chordata has been the development of the fovea. While it would be difficult for the chordate eye to improve its resolution at all field angles without increasing the requirements on both the optical system and the signal processing system exorbitantly, it is possible to increase the resolution significantly over a small area. The fovea is the solution to this desire. In this local area, the signal processing work load is raised by the square of the increase in resolution. The fovea has evolved in many different and unique topologies. The fovea of human is one of the simplest. These foveas are closely related to the niche of the animal. They range from dual fovea in many birds of prey, particularly of the fast diving type, to strip fovea occupying a significant angular extent in the field of view. Dual fovea are also found in *Reptilia* and *Pisces* (fish). Prince[70] has tabulated the foveal characteristics of many chordates.

Some frogs, generally of the family *Ranidae* in *Amphibia Salientia* and frequently portrayed in popular stories, have proceeded in the opposite direction. They are highly optimized for wide angle searching and food acquisition by means of an extendable tongue. Their eyes have a wide field of view. They normally do not move and do not find imaging a useful function while feeding. While feeding, their eyes are not vibrated rapidly to form an image. This aids in their feeding while minimizing their signal processing requirements associated with their wide field of view. It also insures their food is always fresh. They rely on the motion of their prey to generate a trace in their perceptual field. From this trace, they can calculate the trajectory of the prey and from this the general characteristics of the prey, i. e., trajectory, approximate mass and possible type (by short term deviations in the trajectory). When not feeding, they can vibrate their eyes in order to image. It is interesting that many cats, family *Felidae*, appear to share the capability to control the vibration (tremor) of the eye. Most people have noted the characteristic change in mode when a cat is hunting or playing with its wounded prey. It appears that the ability to control the amplitude and possibly the frequency of the tremor is a component of psychological concentration among many vertebrates.

As with *Mollusca*, *Chordata* has developed special optical features for its members living in the transition zone between the aquatic and terrestrial environment. These will be discussed in **Section 1.7.1.4.**

1.2.1.5.2 An invertebrate chordate

[70]Prince, J. (1956) Comparative anatomy of the eye. Springfield, IL: Charles C. Thomas pg. 52

There is a minor subphylum of chordata that lack two of the three main features of chordata. Until 1866, they were considered part of *Mollusca*. Some of them have an outer tunic containing cellulose. Although only partly explored, some of the family have a primitive form of a complex eye with a retina that is neither direct nor inverse with respect to the direction of illumination, but lateral. This specimen was explored extensively in the 1960's[71]. The geometry of its photoreceptor cells will be discussed in detail in **Section 4.2.1**.

1.2.1.5.3 A chordate with cartilaginous vertebrate-sharks

While sharks are occasionally described as invertebrates because of their lack of bones (particularly boney vertebrae), they are clearly chordates in morphological arrangement. Their eyes are similar to those of other chordates. They are generally listed as members of the fish family, *Pisces*, but distinctly separate from the "boney fish." There has been a long debate over whether these animals are degenerate or primitive fish.

Recently, it has become clear that sharks operating in polar seas are able to increase the temperature of their critical systems relative to the water temperature; ***the sharks are endothermic***.

1.2.1.6 The phylogenic position of *Homo sapien*, humans, versus other primates?

The following three subsections remain speculative, even though citing experienced professionals. The field of genomics has opened whole new avenues of exportation relative to the question; *Should Homo sapien still be considered a member of the Order, Primate, when it does not even share the same number of chromosomes with that Order?* Appendix ZK provides a brief listing of the number of chromosomes in different species. It is interesting to note that in 2019, the academic literature lists no other species with 23 chromosome pairs (total 46) except the Guppy (*poecilia reticulata*) and Reeve's muntjac, a small deer (Order *Artiodactyla*, Family *Cervidae*, Species *Muntiacus*). All other primates have 24 chromosome pairs.

1.2.1.6.1 Order Primate focused on the human prior to 2000

> This Section was originally prepared based on the academic literature of and before 2000. Since then significant developments in the field of genetics has been revolutionary in many ways. It has even led to the question, "Is *Homo sapien* still a member of the *Order Primate*?" (**Section 1.2.1.6.3**).

The Order Primate is characterized by a distinctive (crenelated) cerebral cortex overlaying the "old brain" found in lower chordates. The Order Primate includes 12 families, 52 genera and 181 species according to a recent source, Peters & Rockland[72]. While they explicitly use the above hierarchy under the tabular heading Primates, they do not use it within the same hierarchy. They switch to suborders, families and species. Hickman has used the sequence Orders, suborders, super families, families and species. This is indicative of how disorganized the field of taxonomy remains to this day. Because of this confusion, the following paragraphs can only be considered illustrative–but based on Hickman as stated earlier.

Anthropoidea is the suborder of the apes, monkeys and humans. The suborder is frequently divided into both species and a description of their origin. Of the families in this sub-order, there are two super families. The first consists of the monkeys and lesser apes and the second contains the great apes and humans. The designation of humans gets awkward since man is the only species, *Hominoidea*, within the family, *Hominidae*. Some authors have labeled humans more generically as Old World Anthropoids (sometimes labeled Old World Primates). These labels should be differentiated from the Old World Monkeys and may still be inappropriate. The terms Old and New are not used in taxonomy as many would guess. The Old World refers to Asia in this context with the New World including Africa. *However, many in the field interpret the New World to represent the Americas.*

The fall 2019 listing in Wikipedia, granted a poor source, describes New World Monkeys in confusing terms.

> "New World monkeys are the five families of primates that are found in the tropical regions of Central and South America and Mexico: Callitrichidae, Cebidae, Aotidae, Pitheciidae, and Atelidae. The five families are ranked together as the Ceboidea, the only extant superfamily in the parvorder Platyrrhini.[3] Platyrrhini means flat-nosed, and their noses are flatter than those of other simians, with sideways-facing nostrils. Monkeys in the family Atelidae, such as the spider monkey, are the only primates to have prehensile tails."

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[71]Eakin, R. & Kuda, A. (1971) Ultrastructure of sensory receptors in ascidian tadpoles. *Z. Zellforsch*. vol. 112, pp 287-312

[72]Peters, A. & Rockland, K. (1994) Cerebral Cortex, Vol. 10, Primary Visual Cortex in Primates. NY: Plenum, pp xix-xx

In the next paragraph, it notes (presumably including all five of the above families),

> "New World monkeys are the only monkeys with prehensile tails—in comparison with the shorter, non-grasping tails of the anthropoids of the Old World."

Both of the above paragraphs can not be correct.

The eyes of *Anthropoidea* exhibit several unique features and limitations on their performance. These eyes have evolved to provide a simultaneous field of view of slightly more than 180 degrees in azimuth and a maximum of less than 90 degrees in elevation. They do this while maintaining a significant area of stereoscopic vision that includes a fovea of about 6.26 degrees diameter. The fovea and the accommodation provided by the optical system are critical to the visual performance of these animals. Most appear to exhibit a smaller, high acuity, foveola (of nominally 1.2° diameter) within the fovea. It leads to their ability to examine fine details of objects.

Figure 1.2.1-16 describes the primates from the perspective of vision. It is a hybrid of the terminology of Hickman and that proposed by M. Goodman of Wayne State University Medical School. The precise reasoning is based not only on the eyes but also the signal processing within the central nervous system. The particulars of these systems will be addressed in **Chapters 15, 16** & **17**. Goodman estimates *Hominidae* and *Pongidae* diverged about 6–7 million years ago. Similarly, *Homo* and *Pan* diverged about 5-6 million years ago. It has been particularly difficult for the community to define the internal nodes (ancestors) along the medial line. This has led to many investigators to use classification names for nodes along this line rather than specific animal names. The node labeled *Hominidae* is an example. Contemporary thought suggests a common ancestor must link *Homo* and *Pan.* This ancestor is totally conceptual at this time. The terminal nodes are easy to identify. Those shown contain currently existing species.

Ruse, M. & Travis, J. have recently provided a variety of comparisons between members of *Anthropoidea*[73] related to the nervous system, particularly the size of the cranium over time, and many developmental aspects of the human. Unfortunately, they do not compare the genomic codes of the members of the family (see **Section 1.2.1.5.5** below).

[73]Ruse, M. & Travis, J. *eds*. (2009) Evolution Cambridge, MA: Harvard Univ. Press

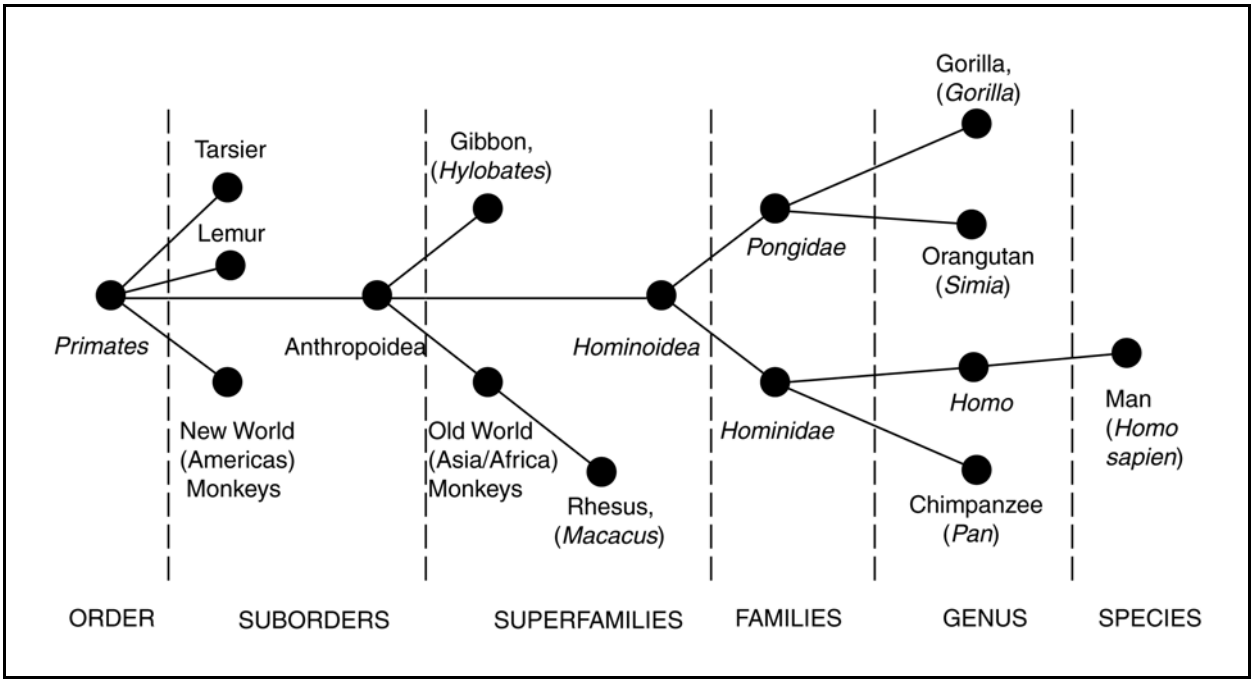

Figure 1.2.1-16 The primate order from the perspective of vision ca. 2008. Later chapters will support this particular phylogenic arrangement up through the family level. The New World Monkeys have prehensile tails and non-opposable thumbs. Tho Old World Monkeys have four opposable thumbs and non-prehensile tails. The position of the Gibbon in this figure is particularly ambiguous. The Gibbon, *Hylobates*, and *Hominoidea* lack tails. *Pan* is reported to have a thalamus (critical to visual performance) most closely approximating that of *Homo sapiens*. However, this report did not include the orangutan in the comparison. See text.

Marx has recently provided a broad ranging popular review of the Phylogenic Tree similar to that above[74].

At least humans have an additional specialized area within the fovea. This foveola, of 1.18 degrees diameter, is critical to the ability of the human to interpret even finer detail than most members of *Anthropoidea* and to read. The foveola is a major component of the Precision Optical System, POS, parts of which were previously labeled the auxiliary optical system of the brain. The POS is a high performance, two-stage, sampled-data servo system that includes the oculomotor system. This system plus the angular capability and agility of the human eyes separates them from all other *Hominidae* (with the possible exception of *Pan* (chimpanzee).

The eyes of the larger *Hominidae* are limited in their spectral response in the ultraviolet region. This limitation is imposed primarily by the thickness of the lens group required to accommodate the terrestrial habitat of these animals[75]. The lens group imposes a short wavelength limit near 400 nm due to its high absorption at shorter wavelengths. As for all *Chordata* examined to date, the actual spectral sensitivity of the human retina includes the ultraviolet, even in maturity. Specific data demonstrating the ultraviolet sensitivity of the human retina is available in **Section 17.2.2**.

Because of the restricted vascular paths to the ocular globes, the vascular system plays a major role in defining the temporal response of the eye. The blood flow, and therefore the energy supply used to operate the eye, is highly tailored within the ocular structure to optimize the performance of the eye. Furthermore, the sensing portion of the eye is fed by two separate paths; the vitral portion of the retina by one branch and the scleral portion (the RPE) by a second. If these facts are not recognized and understood, the temporal performance of the eye cannot be described in any scientifically precise (mathematical) sense.

A fourth feature will require more development later; the operation of the eye-brain system is such that the perceived image is not directly related to the line of sight of the eye. The perceived image is in fact computed in

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[74]Marx, V. (2003) All in the family *Genomics Proteomics* Nov/Dec pp 18-23

[75]Gaydon, A. (1938) Proc. Phys. Soc. (London) vol. 50, pp. 714-720 has shown that aphakic humans exhibit considerable sensitivity in the Ultraviolet, similar to that of insects.

inertial space relative to the earth. Significant motion of the head, or the rest of the body, will generally cause the "clearing of the visual memory" very similarly to that associated with a major rotation of the eye ball. The data processing portion of the brain is closely linked to an inertial platform that helps it create the perceived image of the external world.

Finally, it is interesting that the iris of some "blind people" continues to respond to changes in light level, and even the sensing of motion in the external field (and sometimes sensations of color. Apparently, portions of the Thalamus continue to function in the case of cortical blindness. See blindsight in Section 18.8.11.

1.2.1.6.2 *Hominidae* as a distinct variant within the great apes of *Anthropoidea*

There are significant differences in the brains of the great apes and man, compared to the brains of the lesser apes and monkeys. The difference is primarily in the midbrain. The midbrain is also the least studied and most difficult to study. **Chapter 15** will show that the pulvinar of the midbrain is far more developed in man than in any other species, family, super-family, etc. It is a key element in the ability of man to read and analyze fine spatial detail in object space. Only a few of the great apes in the family Pongidae, the Gorilla, *Gorilla* , the Orangutan, (prior to 1929, *Simia*, now *Pongo*[76]) and the chimpanzee, *Pan*, can approach the human in these areas. When studying reading and the analysis of fine detail, the lesser apes and monkeys are not homologous with humans. There has been a recent proposal to move the chimpanzees, *Pan troglodytes* and *Pan paniscus* from the family *Pongidae* into the family *Homo* based on their degree of similarity in DNA (claimed to be 99.4%)[77]. While one of the most capable of the family *Pongidae*, the chimpanzee, *Pan troglodytes*, still appears inadequate compared to *Homo Sapiens* in these areas. It should also be noted that 99.4% is not a particularly close match being that about 96% is shared by all members of *Mammalia*.

In 2004, Preuss[78] presented a cladogram of these relationships based on the specific characteristics of a particular layer, 4A of the visual cortex, Preuss did not address the place of gorilla, *Gorilla*, in this cladogram, probably due to the limited data due to ethical considerations. He showed, *homo, pongo* and *pan* on the same leg of the chart.

In 2009, Ruse, M. & Travis, J. page 261, say latest findings put the human with gorrila and Pan (chimpanzee) instead of with orangutan. However, their evidence appears to be largely a repeat of that of Goodman.

Even more recent evidence (2011) is key to confirming the close link between humans and orangutans. The decoding of the complete genome of the orangutan has introduced additional consternation. Alice Park of Time magazine has reported, "while humans, apes and chimps share a common ancestor, *Homo sapiens* and orangutans retain genetic traits that have been lost by primates species more closely related to us[79]." This statement reflects old school thinking. What is actually said is, while humans, apes and chimps share a common ancestor, the group consisting of humans (*Homo sapiens*) and orangutans (Pongo) show maximum commonality based on their genomic code and have evolved beyond the other members of the group. Two researchers from Denmark highlighted this situation, "In the process (of evolution), chimps for mysterious reasons lost some orangutan DNA that humans retained[80]." Gaining relevant code only requires a few mutations. Losing code is much more difficult and has not been shown to occur to date.

Placing *Homo* and *Pongo* in the same group on the phylogenic tree as in **Figure 1.2.1-17** obviously causes problems in the names beginning at the family level. Transposing *Pongo* and *Pan* at the genus level while maintaining the family names is the obvious solution. This transposition has been proposed many times previously based on lesser evidence. The transposition leaves *Hominidae* with only two families. As seen, the designation of sub-species in the case of the orangutan is little different than racial, or even ethnic designations in humans.

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[76]- - - - (1929) Opinion 114, International Commission on Zoological Nomenclature. *See also* Schwartz, J. (1988) Orang-utan Biology. NY: Oxford University Press pg 11

[77]Goodman, M. (2003) Natural Selection's Role in Shaping 99.4% Nonsynonymous DNA Identity Between Congeneric Humans and Chimpanzees, *Proc Natl Acad Sci*. May 19, article #2172

[78]Preuss, T. (2004) Specializations of the Human Visual System: The Monkey Model Meets Human Reality *In* Kaas, J. & Collins, C. *eds*. The Primate Visual System. NY: CRC Press Chapter 10, page 241

[79]Park, Alice (2011) Humans' closest genetic kin, Time Magazine, February, 14, 2011. NY: Time-Warner

[80]Locke, D. Hillier, L. et al. *more than 100 names* (2011) Comparative and demographic analysis of orang-utan genomes *Nature* vol 469, pp 529–533

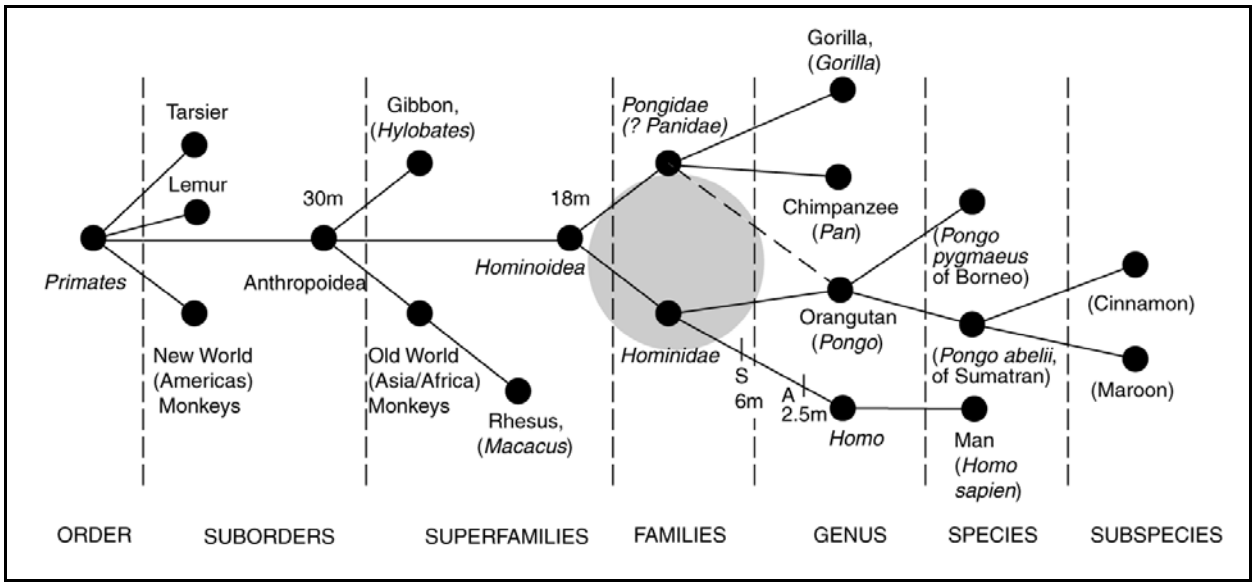

Figure 1.2.1-17 The primate order from the perspective of vision ca. 2010. This reorganization of the phylogenic tree of Primates follows the latest genomic code revelations. It now employs the percentage similarity in the genomic code as a primary factor. The family name Pongidae is replaced by Panidae and the dashed line is no longer functional. Pong is shown with two species, who developed over time (probably less than 2 million years) on opposite sides of a prominent body of water.

The report by Parks was based on the release of a major study by Locke and 101 co-authors (including two with the surname, Fulton but not related to this author) published in Nature on 27 Janurary 2011[81]. This major study of the orangutan is at the cutting edge of science. The results are presented with a strong homocentric aspect with a major suggestion that the orangutan and human parted ways 14-15 million years ago which is consistent with the above figure. However, they conclude that the chimpanzee and gorilla remained part of the human branch of the phylogenic tree until much later (4-5 million years ago for the chimpanzee) when they separated through degeneration, the loss of segments of genetic code that remained in the human genome. Their analysis would have *Panidae* separating from the family *Hominidae* (rather than the super-family, hominoidea) as little as 4.5 million years ago, during the time of Lucy and other pre-humanoids. Efforts to clarify this situation involves ongoing efforts to complete the genome of *gorilla*. Citations 26 & 29 of the Locke et al., among others, discuss some of the underlying assumptions concerning their overall results.

Collins et al[82]. made a recent assertion that the early primate, "*Tarsiers*, which are currently considered to constitute the sister group of anthropoid primates, exhibit a number of morphological specializations such as remarkably large eyes, big ears, long hind legs, and a nearly naked tail." They are also minuscule in size (120 to 134 grams) relative to anthropoid primates according to Collins, et al. "They were originally misclassified as a rodent or an opossum, and even today, their phylogenetic position relative to other primates is under debate. "

1.2.1.6.3 Start of the DNA revolution– IS *HOMO SAPIEN* A PRIMATE?

Homo sapien has 23 pairs of chromosomes while all (other) primates have 24 pairs. By combining the 2nd and 3rd chromosomes of primates into a single 2nd chromosome of man, *in other than a head to tail manner*, a wide panoply of differences in the phenotypes are possible based on the new genotype.

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[81]Locke, D. & 101 co-authors (2011) Comparative and demographic analysis of orang-utan genomes *Nature* vol 469, pp 529–533

[82]Collins, C. Hendrickson, A. & Kaas, J. (2005) Overview of the Visual System of Tarsius *Anatomical Rec Part A* vol 287A, pp 1013–1025

Along with the recognition that the human, *Homo sapien*, has a different number of chromosomes than all other primates, and the recent reappraisals of how to anylyze the variations among the chromosomes of the primates, *little can be said about the actual cladograms shown above dating from the 20th Century.*

Quoting Fan et al[83]., (2002) in the first line of their Abstract,

> "Humans have 46 chromosomes, whereas chimpanzee, gorilla, and orangutan have 48. This major karyotypic difference was caused by the fusion of two ancestral chromosomes to form human chromosome 2 and subsequent inactivation of one of the two original centromeres (Yunis and Prakash 1982). As a result of this fusion, sequences that once resided near the ends of the ancestral chromosomes are now located in the middle of chromosome 2, near the borders of bands 2q13 and 2q14.1."

Based on this fact, it is not clear that humans should be considered as a member of the primates. Furthermore, the fanciful name "junk" bestowed on stretches of DNA code not understood at the time, has now been found to be extremely important. *It is now recognized that the DNA code is much more important than just coding for proteins.*

It is suggested that even the Atlas of Mammalian Chromosomes[84] published in 2013, may need to be carefully analyzed for timeliness since the volume was first released in 1969 via Springer.

The technical language used in current studies requires a true specialist to interpret it. However, Fan et al. make the clear statement,

> "This gross karyotypic change may have helped to reinforce reproductive barriers between early *Homo sapiens* and other species, as the F1offspring would have had reduced fertility because of the risk of unbalanced segregation of chromosomes during meiosis."

This statement plus the recognition that the fusing of two chromosomes within the genotype DNA may lead to an unbelievable number of other changes in the phenotypes. ***These potentials are not even completely categorized at this time.***

The 2011 work by the school of Hobolth et al[85]. and Mailund et al[86]. illustrates the state of complexity recognized at this time.

Hobolth et al. begin their Discussion with,

> "Our analyses find that for ~0.8% of our genome, humans are more closely related to orangutans than to chimpanzees. Incomplete lineage sorting, ILS, between human, chimpanzee, and gorilla is well established, and we show ILS to occur very far back in time."
>
> ". . .The analysis of changing genealogies along the chromosomes using a hidden Markov model provides evidence for independent lines of descent reaching back to the human– chimpanzee–orangutan ancestor, thus allowing observation of the three possible coalescent genealogies that we observe as ILS. Observation of independent descent all the way to the orangutan speciation time implies that the effective population size has been large throughout this period of 8–10 Myr, in particular, the human– chimpanzee ancestral species cannot have experienced a severe bottleneck within this period. Our study is the first to benefit from molecular data in the estimation of the time since the human and orangutan lines separated. Genomic divergence and species divergence are in general difficult to separate, and genomic divergence always occurred further back in time than species separation. This difference between the time of separation and that of divergence is the cause of ILS, and because ILS is a population genetic phenomenon, the observation of ILS allows us insight into properties of the ancestral population."

Mailund et al. begin their Abstract with,

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[83]Fan, Y. Linardopoulou, E. Friedman, C. et al. (2002) Genomic Structure and Evolution of the Ancestral Chromosome Fusion Site in 2q13–2q14.1 and Paralogous Regions on Other Human Chromosomes *Genome Res* vol 12, pp 1651–1662

[84]Hsu, T. & Benirschke, K. (2013) An atlas of mammalian chromosomes. Google Books

[85]Hobolth, A. Dutheil, J. Hawks, J. et al. (2011) Incomplete lineage sorting patterns among human, chimpanzee, and orangutan suggest recent orangutan speciation and widespread selection *Genome Res* vol 21, pp 349–356

[86]

> "We search the complete orangutan genome for regions where humans are more closely related to orangutans than to chimpanzees due to incomplete lineage sorting (ILS) in the ancestor of human and chimpanzees. The search uses our recently developed coalescent hidden Markov model (HMM) framework. We find ILS present in ~1% of the genome, and that the ancestral species of human and chimpanzees never experienced a severe population bottleneck. The existence of ILS is validated with simulations, site pattern analysis, and analysis of rare genomic events. The existence of ILS allows us to disentangle the time of isolation of humans and orangutans (the speciation time) from the genetic divergence time, and we find speciation to be as recent as 9–13 million years ago (Mya; contingent on the calibration point)."

Much work remains before a dependable cladogram can be defined.

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Figure 1.2.1-18 describes the obvious differences between the critical differences in the merger of chromosomes 2 & 3 of the primates to form chromosome 2 of humans, *Homo sapiens*.

http://www.gate.net/~rwms/hum_ape_chrom.html provides an extended discussion of these differences in 2003 by Steven Carr. It is not at that domain in 2019.

The differences are more complex as illustrated in the 1982 paper of Yunis & Prakash[87].

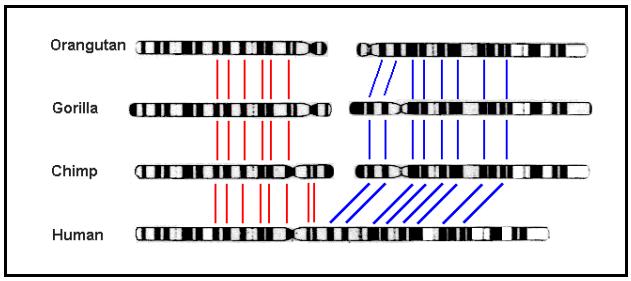

Figure 1.2.1-18 Human versus primate chromosomes. The #2 chromosome of humans appears to be formed from a merger of chromosomes #2 & #3 of the primates. From Wikipedia.

1.2.1.7 Comparison of eyes

Many attempts have been made to compare and categorize the various animal eyes. This has been extremely difficult because of the great diversity found among the eyes. These comparisons have generally focused on only one or a few parameters. There have been so many attempts to provide labels for the different types of eyes that it makes even a review of the literature difficult. What is a simple eye in one text is a completely different eye in another. The goal here is to develop a set of labels consistent with both a majority of the literature and a set of fundamental optical principles. An initial set of labels is provided in **Section 1.2.4** for purposes of discussion. However, the justification for these labels will be found in subsequent sections.

Envy is the initial reaction of a sensor system designer when he looks at the eyes found in nature. The degree of optimization is impressive at every evolutionary level. Each newly emerging phylum, species and family builds on the technology in use during that Epoch, only introducing changes that optimize the new animal to suit its environmental niche better. At every stage, tradeoffs have been made between the demands of available space, data processing, technology, etc. Many of these tradeoffs cannot be recognized based only on morphological considerations. As an example in Copilia, the oscillating rhabdoms move in opposite direction. This not only requires only one muscle, it maintains the inertial state of the animal and prevents it from moving through the water in a pattern dictated by the shifting mass of the lens/rhabdom assemblies.

One of the most interesting and least recognized of the design tradeoffs is that between luminous sensitivity, sensitivity to motion, and total filed of view. It is little recognized but the high degree of feedback used in the adaptation amplifier of virtually every biological photoreceptor precludes the eye recognizing absolute levels of illumination. This has a profound consequence. Any eye of the simple, compound or complex type, is blind to the constant illumination levels in its field of view unless a change occurs in that field. Lacking a change in the light falling on an individual photoreceptor, no signal is produced after a short interval (measured in seconds in man). Thus, the nominal eye is actually a change detector and not an imaging device. It is a starer and achieves maximum sensitivity through its long integration interval. This situation is quite adequate in many animals who wait for their food to come to them. However, in the predators and gatherers, it is a difficulty. A technique must be introduced to create a constant change in the illumination falling on an individual photoreceptor if an image is to be obtained. This is done in the higher animals through the muscular action labeled tremor. The amplitude and frequency of the tremor are just large enough to cause a significant change in the instantaneous illumination level on each photoreceptor. For high contrast environments, the angular amplitude of the tremor reflected into the object field

[87] Yunis, J. & Prakash, O. (1982) The origin of man: a chromosomal pictorial legacy *Science* vol 215(4539), pp 1525-1530 DOI: 10.1126/science.7063861

need not be as large as one pixel. This is the explanation of the super resolution of the human eye compared with the pixel size of its photoreceptor cells. Animals that do not exhibit a tremor frequently introduce relative motion by moving their head after detecting motion in their visual field. This design tradeoff plays an important part in the description of eyes found in the animal kingdom.

Wolken has provided a widely reproduced summary of some eyes found in different phylogeny. He has published variants of this figure in at least 1966, 1971, 1975 & 1986. The purpose being to provide a cursory comparison of the geometries employed. A similar summary, using the layout of Wolken (1975, fig 13-1), is presented in **Section 1.2.4** following the discussion of some optical features found in different phyla, species and families.

As mentioned earlier, Hughes[88] has provided a tabulation of eyes by axial length as a function of body weight in *Chordata*. The data is interesting because the length of the eye only varies over two orders of magnitude while the body weight varies over seven orders. The length of the eye is indicative of the limiting angular resolution of the eye. It is the ratio of the length to the diameter, the f/#, of the eye that is indicative of its sensitivity to radiation.

1.2.2 Correlating genetic and phylogenic data

The correlation of genetic and phylogenic information is probably the ultimate subjective linking of conceptual data based on limited observational data and incomplete models. It requires the greatest knowledge and precision across disciplinary boundaries. The concept is quite clear but the field is quite new. *Epigenesis* is the creation of a physical organism, the *phenotype*, from a specifically encoded copy of a DNA molecule, the *genotype*. The process is exceedingly complex, involving the manufacture of proteins, the replication of the DNA, the replication of cells, the gradual differentiation of cell types and so on. Within the DNA are segments of the molecule assumed to influence uniquely specific features of the *phenotype*. The assumption is based on statistical relationships between observed abnormalities in *phenotypes* and changes from the norm in the *genotype*. There is the further assumption that the observed changes in the *phenotype* are uniquely due to the observed change in the *genotype*. This requires a linear transform from one set of characteristics in the genotype to a second set of characteristics in the phenotype--an exceedingly unlikely assumption. Hofstadter[89] addresses this concept. He points out that in one of the only genomes fully decoded, of the tiny virus, ϕX174, some of its nine genes overlap. Two distinct proteins are coded for by the same stretch of DNA. There is even one gene contained entirely within another. Clearly the *genotype* reader does not read a single amino acid at a time. The reader employs correlation, and even memory, techniques when reading a specific piece of DNA. It is known to read the nucleotides in groups of three. Therefore, knowing exactly where it started reading can be important.

The epigenesis of an animal based on such simple encoding would be highly unlikely based on the complexity of the sequence of events listed above. The process appears to involve state variables that are highly recursive. Hofstadter differentiates between the “prosaic” isomorphism represented by such simple one to one transformations and the more exotic isomorphism likely to be involved in epigenesis.

A recent paper illustrates some of the difficulties[90]. As in most papers, an introduction is provided that is heavily influenced by the conventional wisdom associated with only a few schools in each discipline. Many of the assumptions are controversial and provided without foundation references. This can lead later investigators down questionable paths at great economic and temporal expense. When reading the above paper, it is important to note that the visual process in animals (including humans) is based on photoreceptors sensitive to **four** (not three) separate spectral regions. These regions are the ultraviolet, short, medium and long wavelengths of vision. The peak sensitivities of these four photoreceptors are at: 342, 437, 532 & 625 nm. Although the scotopic luminosity function of the human exhibits a peak near 500 nm, and the isotropic absorption spectrum of the Rhodonines peaks near 500 nm (491 to 503 nm based on various reports), this is a coincidence. There is no functioning photoreceptor in any eye with a peak response at this wavelength. As will be shown, the scotopic luminosity function is a perceptual response based on computation within the visual system. The photoreceptors of vision employ an anisotropic absorption characteristic due to the structure of the absorbing material.

Because of the lens in the human eye, and the eye of the larger chordates, man is unable to observe the ultraviolet spectrum except in unusual circumstances. However, the human retina does contain all four spectral photoreceptors.

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[88]Hughes, A. (1977) The topography of vision in mammals of contrasting life style. In, Handbook of Sensory Physiology, Vol. VII/5 Crescitelli, F. ed. Berlin: Springer-Verlag pp. 613-756

[89]Hofstadter, D. (1999) Godel, Escher, Bach: an eternal golden braid. 20th anniversary Ed. NY: Basic Books, pg. 159

[90]Yokoyama, S. (1994) Gene duplications and evolution of the short wavelength-sensitive visual pigments in vertebrates. Mol. Biol. Evol. vol. 11, pp. 32-39

This is easily demonstrated by the aphakic human who has had the lens removed (See **Section 17.2.4)**. His luminosity function clearly shows the presence of an ultraviolet sensitive photoreceptor. Because of this capability, any discussion of the number of genetic sites related to the spectral performance of the photoreceptors should recognize the requirement to accommodate **four** separate spectral absorbers (omitting any possible achromatic photoreceptor for the moment). Using his terminology, the geneticist must be aware of the potential presence of the UVWS (ultraviolet wavelength sensitive) pigment in the chordate eye. Recognition of the existence of these four types of photoreceptors in the retina, even if not normally observed in optometric examinations, leads to the redefinition and rearrangement of the four genetic clusters associated with the spectrum of vision.

With the understanding that there are no physical photoreceptors in the visual system that can be described spectrally by the designation "rod" (**Section 3.1.5**) and that the human eye contains ultraviolet sensitive receptors, the paper by Das, et. al[91] contains a useful list of references to the genetic sequencing related to the visual process in animals.

Interestingly, a single error in the genotype is not likely to account for red-green color-blindness because this psychophysically observed anomaly appears in at least **two** forms. In the first, the anomaly is not accompanied by an abnormal photopic luminosity function. Clearly such an anomaly cannot occur in the photosensitive channels of vision and it does not involve the chromophores of vision. In the second anomaly, the photopic luminosity function is affected. Clearly, the second anomaly can be caused by a failure in the photosensitive channels of vision, the photoreceptors, or in the chrominance processing channels of vision. Each of these channels contains dozens of individual circuit elements besides the chromophores. An error in the formation, connection or operation of any of these elements can cause the observed error. It is not likely all these possible errors are caused by a single abnormality in the genotype. This is particularly true regarding red-green color-blindness that has also been linked to environmental problems during pregnancy, namely scarlet fever and other fever conditions.

1.2.2.1 Inadequate determination of spectral sensitivity

The literature contains a large variety of studies attempting to define the spectral performance of different families, species and phyla using inadequate techniques. Often, psychophysical techniques have been used that can more accurately be described as behavioral studies. In many of these studies, a visual spectral response for the animal has been obtained that is broad, exhibits a spectral peak in the interval between 500 nm and 555 nm and also exhibits inflection points or relative maxima. Historically, the investigator has announced that the animal is therefore achromatic and only has one spectrally selective class of photoreceptors. This class is claimed to be that of rods based on the above spectral characteristic. As will be shown in this work, a spectral response such as that defined above is typical of that obtained for human over either the photopic, mesopic or scotopic illumination regions. This broad spectrum is created from the contribution of three separate and distinct chromophores in all but the scotopic region. In the scotopic region, the observed spectrum is created from the contribution of only two chromophores[92].

1.2.2.2 Changes in spectral performance with evolution

Periodically, essays appear in the literature attempting to describe the order of appearance of the various spectral bands in a given species or phylum over time[93]. These tend to be based on behavioral observations of only a small segment of the species population over a limited length of evolutionary time (the last 50 years). Ahnelt et. al[94]. have recently produced a web site that discusses this subject from a curious perspective, which has been addressed by others. Their premise is that the visual spectrum of various chordates has evolved significantly based on their ecological niche. One of their axioms is that "Primate trichromacy is the exception not the rule." They proceed to the corollary that most mammals, with the exception of some primates have, in addition to rod receptors, only two spectral types of cones. As a result, they claim these mammals are dichromats and only able to discriminate variation between blue and green. Their simple approach fails when *they* point out that some rodents exhibit ultraviolet sensitivity instead of blue sensitivity [sic]. Bowmaker[95] has also attempted to define trichromacy as a recent innovation among the primates with the rest of the animal kingdom still primarily dichromatic. Any report

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[91]Das, D. Wilkie, S. Hunt, D. & Bowmaker, J. (1999) Visual pigments and oil droplets in the retina of a passerine bird, the canary *Serinus canaria*: microspectrophotometry and opsin sequences. Vision Res. vol. 39, pp. 2801-2815

[92]Helson, H. (1943) Some factors and implications of color constancy *J Opt Soc Am* vol 33(10), pp 555-567

[93]Crescitelli, F. (1972) The visual cells and visual pigments of the vertebrate eye, *In*, Handbook of Sensory Physiology, Vol. VII/1, Dartnall, H. *Ed*. Photochemisty of Vision, NY: Springer-Verlag. pp 264-267

[94]Ahnelt, P. Glosmann, M. & Schubert, C. www. univie.ac.at/Vergl-Physiologie/www/gphy_marsuprod.html (1999 to date)

[95]Bowmaker, J. (1998) Evolution of colour vision in vertebrates. Eye, vol. 12, pp. 541-547

claiming an animal only exhibits one broad spectral channel in its visual spectrum should be discounted out of hand. Even claims of dichromacy as the limit of development should be discounted until demonstrated more carefully. As hinted at above and to be confirmed below, virtually all animals exhibit full color vision. Many experimenters confirmed the color vision of animals beginning as early as the 1920's by performing color constancy experiments.

This work takes the opposite corollary based on the same axiom. The Primates, and other large chordates, are *limited to trichromatic vision* due to absorption in their outer lens-group, while the smaller chordates and other phylum are capable of *tetrachromatic vision*. The transition during the life of a particular animal may be due primarily to the growth in the size of its eyes and therefore the increased absorption of their outer lens group. There are suggestions that the ultraviolet receptors may atrophy in these animals as they grow. However, there is very strong evidence that the ultraviolet cells do not atrophy in humans. The evidence is from a 54 year old aphakic researcher within the vision community.

This work suggests that tetrachromatic vision has been available in the animal kingdom for more than 500 million years, at least as far back as the evolution of *Limulus* and the ancient insects. Backhaus, et. al. suggest the same number based on their reading of paleontological and phylogenetic evidence[96].

This work also demonstrates that there are no achromatic or high luminance sensitivity photoreceptors known colloquially as rods. Rod is a morphological label that plays no role in the physiology of vision. See **Section 3.1.5**.

> **The ancient and totally archaic Duplex Theory of vision, with rods responding to low light levels and cones responding to high light levels, has been completely falsified and should be purged from all textbooks in a timely manner. The Duplex Theory constitutes a blight on the teaching of biological science.**

1.2.2.3 Correlating spectral response and phylogenic data

Although the literature of the 1950-60's suggested virtually no correlation between the spectral capability of one species versus another, this was never the case. **Section 1.3.3.4** will introduce the spectral capabilities of the different species as a function of their phylogenic family. While considerable diversity has been introduced to satisfy specific niche environments, the overall spectral architecture is quite clear.

1.2.3 Unique position of humans in the visual phylogenic tree

While the human is frequently lumped with the primates when discussing vision, this is unfortunate. While the Primate Order is characterized by its level of brain development, (a very coarse trait), the Order is very inhomogeneous. This situation is continued within the Sub-Order *Anthropoidea*. This Sub-Order contains three super-families, commonly described as the New World Monkeys, the Old World Monkeys and the Apes. When discussing the visual system in total, rather than just the eyes, there are significant differences between these super-families. These differences become major in Chapter 15 that is focused on the cortex.

Even within the Apes, there are significant differences in visual morphology, physiology and therefore capability. The Apes are generally divided into three families, the lesser apes, *Hylobatidae*, the great apes, *Pongidae*, and the family of man, *Hominidae*. There is a significant difference in the level of development among these species centered on the diencephalon of the old brain (*paleo*-cortex). Chapter 15 will show there is an overlay of the Thalamus, the major component of the diencephalon, that is uniquely developed in humans. It is this overlay, coupled with a major expansion of the pulvinar, an element of the thalamus, that separates humans from all other animals. This overlay will be defined as the perigeniculate nucleus/pulvinar (PGN/pulvinar) couple in Chapter 15. It provides the human his unique ability to analyze, interpret, and memorize fine detail. When this ability is concentrated on character sets (alphabets), it provides the human his unique ability to read.

The use of the lower primates in research significantly limits the researchers capability to understand the complete human visual system. Only the great apes approach the capability of *Homo Sapiens* in their capability to analyze fine detail. The order of capability appears to be human, orangutan, chimpanzee, gorilla.

1.2.3.1 The awkward semantics used in discussing the brains of primates

The term primary visual cortex is frequently found in the vision literature. This is unfortunate. The term is used to

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[96]Backhaus, W. Kliegl, R. & Werner, J. (1998) Color Vision: Perspectives from Different Disciplines NY: W de Gruyter pp 177-178

describe the posterior portion of the occipital lobe of the cerebral cortex. It will be seen in Chapter 15, that there is a major question concerning the primacy of this area within the visual system.

The etiology of the expression appears to be as follows:

It was discovered long ago that the rear part of the brain, at the back of the human head, was involved in vision. This became known as the visual cortex. Later, the visual function was found to be concentrated in this area in other primates as well. The area became known as the visual cortex of the primates. In English, this expression can be shortened using the possessive form, resulting in primates' visual cortex. It was not long before this expression was simplified to make it easier to say and communicate. It became the primary visual cortex. Although, the words primate and primary have the same root, the concepts of primates' and primary are distinctly different.

It will be shown, in **Chapters 15** & **18**, that the complete destruction of the primates' visual cortex does not lead to complete blindness. In some cases, subjects with this condition have refused to admit they were blind and went about their normal life. This has led to the clinical condition known as cortical blindness. It highlights the critical (?, primary) importance of the PGN/pulvinar couple in human vision.

1.2.4 Summary

The animal eye takes on three basic forms involving either;

+ the individual simple eye (or ocellus) consisting of a single ommatidia with its associated optical system OR the replication of a complete simple eye into a more complicated compound eye

+ the replication of the photoreceptor element alone behind a common lens such that the illumination strikes the distal end of the photoreceptor cell (a complex eye with a direct retina)

+ the replication of the photoreceptor element alone behind a common lens such that the illumination strikes the proximal end of the photoreceptor cell (a complex eye with an inverse retina)

Each of these three eyes is associated with a different Phyla in the animal kingdom, the *Arthropoda*, the *Mollusca* and the *Chordata* respectively.

Although the last two eyes are both of the complex type and appear very similar in gross anatomy, the added rotational freedom of the chordate eye is very important to the survival of the Phylum in its environment.

Lacking the ability to rotate within a socket, the arthropod eye must rely on other techniques to form a wide angle view of its surroundings. It does this through replication of the basic ommatidium to form a compound eye. Each ommatidium addresses its own field of view through its own dedicated optical system. The result is the well-known mosaic eye of the insect world. This eye cannot image the stationary world around it. It only senses objects moving through its visual field.

The fundamental mollusc eye has evolved as a complex eye with a directly illuminated retina. This eye imitates the chordate eye in overall appearance but lacks several features of the chordate eye. It does not have the rotational freedom of the chordate eye. Therefore, lacking other movement by the animal, this eye would not image a fixed scene. It would only "image" objects moving through its visual field. The eyes of *Cephalopoda* have developed sufficient angular freedom in one plane to allow the use of a tremor to provide an imaging capability.

When discussing the total visual system, the human system exhibits a PGN/pulvinar couple that is unique. This overaly system separates humans from all other animals and can be compared **only** with the equivalent systems of the great apes.

1.2.5 Correlating morphological names and phylogenic data

Correlation of the different names found in the literature for equivalent elements of the visual systems is very useful. Correlations have been prepared by many investigators over the years. Correlations will be offered periodically throughout this work to aid in the overall presentation. These correlations cannot always be definitive because of the wide adaptations used to fit the environmental requirements of different animals. However, the basic comparisons are useful.

Table 1.2.7-1
Correlation of visual elements between Phyla

Arthropoda	Mollusca	Chordata	Comment
Cornea	Cornea	Cornea	Primary optical element in terrestrial chordates
Vitreous body[+]		Anterior humor	
		Iris	Controllable aperture stop
Lens*	Lens	Lens**	Primary optical element in aquatic chordates
Crystalline cone***		Vitreous humor	gelatinous material
		Neural tissue	Field lens in Chordata
Retina(direct)	Retina (direct)	Retina (reverse)	Photosensitive assembly
Retinula			Photosensitive subassembly
Rhabdom	Rhabdom	—****	A morphological group of photosensitive cells
rhabdomin	Rhabdomin	Photoreceptor cell[++]	Photosensitive cell
Rhabdomere	Rhabdomere	Outer Segment	Photosensitive component
Rods	Rods	Disks	Sub-components of Outer Segment
Basal pigment cell	Argentea	Tapetum	Used variously

[+] Stavenga & Hardie (1989), fig 12.
* It should be noted that the proximal lens in *Arthropoda* is an optical element and is inherently ellipsoidal.
****** Weale uses the expression "crystalline lens" for the proximal lens in Human. (Weale, 1961)
***This structure is not in a state of matter associated with crystals. The material is a viscous liquid crystal or gel. Its function is that of a light pipe. Characterizing it as a crystalline cone is archaic. A gel cone or liquid crystalline cone would be more descriptive.
****No readily recognizable grouping of photosensitive cells occurs in the adult chordate eye.
[++]Not including the Outer Segment

1.3 A survey of the state of the art in vision

There are a variety of problems with the conventional wisdom regarding the visual process. Uttal has addressed several of these from the perspective of a generalist in biology[97]. His preface and section on questionable dogma are recommended. As he states, "in spite of the extended historical period of interest in the kinds of perceptual phenomena, there is still a remarkable absence of solid understanding in the field."

1.3.1 Some Simple Reality Checks

Before going too far, exploring some simple arm chair experiments in human vision is useful. This will better enable the reader to evaluate some statements of folklore, found in both the popular and scientific literature, that have risen to the level of an axiom.

1.3.1.1 Adaptation– There is frequent reference to the synchronous adaptation of both eyes in response to a change in light level to either eye. While in a dimly lit room, less than one-half moon outside, close one eye and turn a light on for a few seconds to a minute. Turn off the light. Now observe how much detail you can see with the open eye. Close the first eye and open the other eye. Observe how much detail is visible. Alternate eyes a few times. The level of adaptation is clearly quite different in the two eyes; although looking in a mirror will confirm that the irises of both eyes have contracted to the level established by the eye open to the higher light level. The conclusion is that the irises of both eyes normally operate in synchronism, however, the major adaptation process in vision operates individually in each eye and is independent of the iris.

1.3.1.2 Peripheral Color Vision– Look straight ahead while bringing a reasonably large (1/2 inch square) object of red or blue from behind you into your peripheral field of view. Note the angle when you first see the color of the object. This experiment should clearly show you have color vision at angles greater than 60 degrees from the optical axis, the area limited to "rod" vision in both the scientific and popular literature. The status of "rods" will be developed later.

[97]Uttal, W. (1981) A taxonomy of visual processes. Hillsdale, NJ: Lawrence Erlbaum Associates, pp 721-743

1.3.1.3 Foveal vs peripheral night vision– On a clear night, take your star map and go outside to look at the stars. It is best to be thoroughly dark adapted (at least 20 minutes to be fair). However, the point can be made with less dark adaptation. Our object is to see how much more sensitive our peripheral vision is to our foveal vision. The most sensitive part of our field of view is about five degrees temporally (toward our ears in the horizontal plane) from our point of fixation. This is the location of the optical axis of the eye. The photoreceptors found there are about 50% larger in diameter than in the fovea. Our object is to see what is the dimmest known star we can see using our most sensitive area and using our fovea. Do not use a red star in this initial experiment. Most people will find the difference in stellar magnitude between these two stars is less than one. One stellar magnitude is a factor of 2.5:1. This is a difficult experiment because of the small difference in sensitivity involved. Try using the stars of Ursa Major (the big dipper). Can you see all four stars forming the cup of the dipper with both your foveal and your most sensitive vision?

Clearly, our night foveal vision is not limited by “cones” in the fovea, with a sensitivity 1000 times less than “rods,” as frequently stated in the literature. It is limited by two features. First, it is limited by the smaller cross-sectional area of the photoreceptors in the fovea. Second, it is limited by the poorer performance of the elliptical lenses of the eye five degrees from the optical axis when the iris is fully opened (related to the Stiles-Crawford Effect). The first cause introduces a factor of about 2:1 and the second cause accounts for a factor of less than 1.5:1.

1.3.1.4 Night Color Vision– Step outside on any clear night and look up at the stars. Do you see any colored planets or stars? Mars, “the red planet,” should be easy to see somewhere along the ecliptic if it is in the sky. There are many colored stars, and many of these have names given to them in ancient times. According to the Field Book of the Skies, "There are many tints easily seen with the unaided eye." These usually range from green to yellow to red. Can you recognize the color of a star while looking directly at it? Do you have color vision under low light conditions in your fovea?

1.3.1.5 Eye as a Camera– While looking straight ahead and without moving your head, note closely the field of view you perceive. Without moving your head or blinking, move your line of sight 5-10 degrees to either side and back. Try up and down by 5-10 degrees. Did the overall scene that you perceive move? Would you expect this result if you took a picture with a camera and then took a second picture with the camera turned 5-10 degrees? The process of detecting and perceiving information by the eye will be addressed later.

1.3.1.6 Eye as a Change Detector– During your next eye examination, while sitting at the Visual Field Analyzer[98] --a device that presents a uniform white field to the eye-- repeat a simple experiment fully explored by Yarbus in the 1950's. Before the technician inserts a stimulus into this uniform white field, note that in the absence of any blinking or head movement, you begin to observe a darkening of your field of view after 1-3 seconds. If carefully done, you will become completely blind during this experiment. This is not the normal result obtained with a camera. It is the normal response expected of a sensor that is a "change detector.”

1.3.1.7 Bright Adaptation as opposed to Dark Adaptation– After attending an afternoon movie and becoming fully dark adapted, walk quickly out of the darkened part of the theater into the bright sunlight. Neglecting the pain for the moment, how long does it take before you can see effectively? It probably takes a few seconds, the period required for "Bright Adaptation.” Both "Bright" and "Dark" adaptation need to be considered, explained and quantified.

> **The above simple experiments will be referred to later to help the reader put into perspective and better understand some of the results presented.**

1.3.1.8 Noise Limited performance-- The noise performance of the visual system is too complex to be addressed in this introductory material. However, the general conclusion can be drawn that the visual system is not limited in performance by internal noise. The system is usually limited in dynamic signal range at high illumination levels and by the noise associated with the randomness of the photons in the incident radiation at lower illumination levels. The subject will be addressed in detail in **Chapters 11, 16** and **17**.

1.3.2 Survey of the Literature

It has long been taken as an article of faith in the "hard sciences" and the engineering communities that a discipline was not understood until one could assign numbers to it. This author believes it is time to apply this axiom to the subject of vision as well. This will help remove the large inconsistencies and misunderstandings found in both casual discussion and in the literature, both popular, popular scientific and strictly scientific journals.

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[98] Manufactured by Humphrey, or equivalent.

This problem of specificity is particularly serious in the color vision arena where a great range of data has been collected under a variety of conditions and interpreted inconsistently. The classic example is concerning "rods" and "cones." Various eminent writers have developed conceptual theses that have led to conundrums. As an example,

+ it has been claimed that vision outside the foveal area is mediated by "rods,"

+ it has been claimed that "rods" only contribute to monochromatic (non-color vision),

+ it has been claimed that the fovea is made up primarily of "cones" which support color vision.

On the other hand, it has been clearly shown that the center of the fovea contains "rod" shaped photoreceptors that are variously called "rod-shaped cones" or "color sensitive rods" (see **Section 3.1.5.3**). It also has been claimed that in the very center of the fovea (near or on the point of fixation of the eye), which only contains "rod-shaped photodetectors," humans cannot see color. Yet the Munsell Lantern Test is commonly used to measure low light level color vision at the point of fixation. Any observer is quite aware of the fact that he can see a colored strobe light on an aircraft at night when looking directly at it (along the line of fixation).

This last observation leads to a second conundrum in conventional theory. If color vision in humans disappears at low light levels, why are all emergency vehicle lights flashing colored lights instead of flashing white lights? Why are these lights observed in color even at very large distances?

A separate area of difficulty in the current literature involves the use of light versus electron microscopy to observe detail at or near the spatial resolution limit of the respective technique. Military photo-interpreters get many laughs out of certain photographs taken at or near the limit of a systems spatial resolution capability. In a picture of a railroad track as an example, producing a picture where a railroad tie is missing is quite easy (or an extra "tie" appears). Similarly, pictures of three-bar resolution charts will exhibit either two or four bars in the smallest perceivable three-bar pattern. The effects employed to produce these trick results are usually diffraction and Moiré, and occasionally an effect due to a "spider." A spider is a device introduced into a blocked optical system to support the blocking element. This last effect is not applicable to natural vision. The point is that a microscopist should not only provide a scale in the prints of his imagery, but also a target *in the object field* of his instrument defining the limit of resolution of his system. This is especially important when looking at a sharp high contrast edge and trying to define adjacent fine detail. A specific example involves determining whether a membrane is or is not surrounding the discs of the outer segments of the photoreceptors. If there is, how do the discs exfoliate from the outer segment when they reach the outer end; do they penetrate the proposed membrane? If so, what is the mechanism? Does the membrane end before reaching the end of the disk stack? Alternately, is the dark line, described as the membrane, actually the first diffraction band of light as it passes the sharply focused high contrast edge?

Mathematics can provide a valuable framework in which to place our knowledge in this field and provide valuable lines of demarcation between broad conceptual statements (often progressing to strong positions) presented by various authors. It can also be extremely valuable in defining new and more precise experiments. The results of these experiments can then be added to the knowledge base in an efficient and easily understood way.

Another area of significant difficulty is in semantics. Adopting a related word is natural in science and engineering, possibly with an adjective added to define a new situation. However, a referencing author may delete or change the adjective and by that paint a different picture in the reader's mind. The use of the forms of the word cilium is a particular problem in vision. This is because of its wide use in both vernacular and scientific senses to describe situations somewhat similar to the prototype situation. However, in many cases, these fine features are neural material forming signaling pathways. They are not protein material as in a hair.

A final example is the use of broad color names to describe the primary sensitivity of photoreceptors, as shown elsewhere, the words do not describe the same colors in different languages around the world. Thomas Young is often quoted as saying the middle wave detector was yellow in 1801 and green in 1802. Which is it? These peak sensitivities need to be expressed in numbers that can be derived mathematically and on graphs. To reduce the confusion in his time period, Young summarized in 1807[99],

> "From three simple sensations, with their combinations, we obtain several primitive distinctions of colours; but the different proportions, in which they may be combined, afford a variety of tints beyond all calculation. The three simple sensations being red, green and violet, the three binary combinations are yellow, consisting of red and green, crimson, of red and violet; and blue, of

[99]Young, T. (1807) Lectures on Natural Philosophy

green and violet; the seventh in order is white light, composed by all the three united."

While this quotation clarifies the green-yellow controversy, it also shows he is constrained in his interpretation of the mixture of red and violet and his fundamental trichromatic assumption. This work will show that a mixture of violet (as he interprets the name) and green cannot produce a saturated blue. When speaking precisely, the complete perceived human spectrum requires recognizing that the human retina is tetrachromatic. See **Section 17.3**.

The use of the term tetrachromatic in this Chapter does not include the proposed variants on human vision described by Gavrik[100] or similar variants suggested in *women* due to a genetic mutation[101]. In both cases, the authors suggest the presence of a fourth chromophore in the region between the normal M– and L– channel photoreceptors. However, the proposal is based on psychophysical testing and does not include any electro-physical or other physiological. data.

After 50 years of exploring the *rhodopsin* proposition for defining the chromophores of vision, no record has appeared of a chromophore related to color vision being extracted from a primate. Related to this fact is the fact that no specific chemical formula for any chromophore of color vision in primates has been published.

Long after the detailed exploration of the external membrane of the axon of the squid, no detailed explanation has appeared in the literature of how a complete neuron works and the detailed nature, i.e., an equation, of its transfer characteristic.

Up until now, no detailed explanation has appeared in the literature, i.e., a mathematical equation, for the output current of a photoreceptor as a function of its illumination.

Brown & Wolken, among others have begun to think of the photoreceptors as having properties ascribed to liquid crystals, i. e., respond to light, to temperature, to pressure, to electrical stimulation and to changes in the chemical environment[102].

The journals relating to vision have recently begun to publish focused editions, "Special Editions," on a variety of subjects. These typically contain a series of "reviews" that actually support and frequently provide additional data on the work of one or more particular well known authors in the subject area. These editions seldom include any schematic or block diagram of the visual modality placing the subject matter into context. The introductions frequently end with a description of the inadequacy of the data in the articles relative to the target subject. Several of these will be examined in **Section 1.3.2.7**.

1.3.2.1 The Zone Theory as an abstract mathematical model

For many years, the additive theory of vision championed by Young and Helmholtz was in competition with the subtractive theory of Hering. Beginning with Mueller in the 1930's, a zone (or stage) theory appeared that attempted to merge the most appropriate postulates of the additive and subtractive theories[103]. Although the zone theory has been presented in a variety of mathematical contexts, it has never been presented as a physiological model. Thus, it remains at the conceptual level and is based on linear algebra. At that level, the first zone employed three spectral channels that combined mathematically to form a first set of three intermediate equations (of no physiological significance). The second zone performed an additional series of calculations based on these equations to form an a second set of two intermediate equations (of no physiological significance). These two sets of equations were then manipulated to form three additional equations that equated to some of the observed data. It was surmised that additional zones probably served other functions.

The above computations led to the postulates finally adopted by the C.I.E. as (**but which are not**) fundamental. These included the postulate that the function , $\bar{y}(\lambda)$, was identical to the normal (smoothed) luminous efficiency function. This function is not the spectral response of the mid wavelength chromophore nor does it conform to the absorption spectrum of some achromatic absorber.. It is calculated from the spectral response of the three spectral absorption bands and does not include a component from an achromatic absorber.

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[100]Gavrik, V. (2002) Tetrachromacy of human vision: spectral channels and primary colors *SPIE Proc* vol 2241, pp 315-318

[101]Greenwood, V. (2012) Super human vison *Discover* Special Issue, Jul/Aug pp 29-31

[102]Brown, G. & Wolken, J. (1979) Liquid Crystals and Biological Structures. NY: Academic Press pg 142

[103]Wyszecki, G. & Stiles, W. (1982) Color Science, 2nd Edition. NY: John Wiley & Sons, pg 583 & 634-639

The above formulation results in a highly intertwined relationship between the luminous and chromatic functions of vision. The relationship involves both a set of dependent (as opposed to independent) algebraic equations and a large set of shared but constant coefficients. As currently conceived, the Zone Theory is entirely linear and does not incorporate or accommodate any adaptation mechanism.

1.3.2.2 Derivation of the Photoexcitation/De-excitation equation

The solution of the Photoexcitation/De-excitation (P/D) equation applicable to the photoreceptors of vision is an important example of the requirement to use the proper mathematical methods to solve a given problem. The solution to this process is necessary before the generator potential associated with the photoreceptor cell can be properly interpreted. During the 1980's, many attempts were made to find the mathematical function describing the response of the photoreceptor cell to excitation of different flux level. These invariably failed because they relied on the integral calculus and a few solutions of simple differential equations found in tables. Only through the complete solution of the proper and complete differential equation employing complex variables is the true situation properly characterized. This complete characterization includes both an amplitude component and a time delay component. When evaluated for the correct initial conditions, this solution provides the complete transient solution for the P/D equation including the variable time delay term inherent in the process.

The investigators working in the 1980's struggled mightily with the variable time delay they measured. They could not explain it by using inadequate mathematical tools.

Because of the sophisticated mathematics involved in the development of the P/D equation, several simplified forms of the equation are provided in this work for the benefit of investigators working in various areas of the visual process. These simplifications do not involve approximations, only special cases of the complete P/D equation. Some simplifications offered have provided useful insights when comparing data sets with both the full and simplified forms. These special cases will be annotated in detail.

Because of the rigor required in the development of the P/D equation, negative critical review of this foundation should only be offered by those able to discuss first order differential equations involving complex number arguments. Negative critical reviews of the simplified forms cannot be seriously entertained if the reviewer cannot provide a reinterpretation of or find an error in the underlying complete P/D equation.

Conversely, alternate theories based on;

+ unknown sources of energy,
+ assumed a priori equations,
+ equations only describing the envelopes of families of curves and
+ smoothed curves based on averages of ensembles

should not be considered substantive. Interestingly, many investigators do not seem to know that the current CIE standards rely on all of the above shortcomings. They were developed for use by technicians in the application of light and color and were never put forth as rigorous representations of the vision process.

Building on this foundation of photo-excitation, it is possible to;

+ explicitly predict the four color chromophores of biological vision (humans only use three of the four, whereas some animals use all four (Others animals use a different permutation of three out of the available four),

+ explicitly predict both the photopic and scotopic spectrums of human vision based solely on these spectrally sensitive chromophores and also provide the photopic (and/or scotopic) spectrums for animals like honey bees who see in the ultraviolet portion of the spectrum,

+ explicitly explain the small shift in visual spectrum of euryhaline fishes and other animals who appear to replace their chromophoric molecules as they change environments.

+ explicitly account for the mechannisms used in the visual signal processing path of the animal eye as it evolved starting with the worm and progressing up through the phylogenic tree.

+ explicitly define the pulse encoding technique used to communicate between the retina and the brain.

+ explicitly describe the functional characteristics of visual neurons, both as to their signal propagation characteristics and their amplifier characteristics.

+ provide a specific electronic circuit, using both analogous and equivalent circuit techniques, that rigorously defines the signaling characteristics and the signaling paths used in the eye (including the three hierarchical signal paths; the brightness, the chrominance and the appearance channel).

+ explain explicitly the critical importance of motion in the operation of the eye, and its use over a span of animal taxonomies as required by their environment and niche in the food chain.

+ show conclusively that the eye is inherently not an imaging device but a change detector based on motion (either internal or external to the animal) for its proper operation.

+ provide evidence that external feedback (rigorously defined) as a mechanism plays at least a trivial and probably nonexistent role at the neuron level in biological vision. Where external feedback is proposed in the literature, signal subtraction between adjacent signal channels provides an alternate explanation for the process.

+ highlight the fact that the cognitive "image" formed in the brain of an animal is referenced to the inertial position of the head (in humans at least) and not the position of the eye(s). Thus, the bizarre eye motions of the Chamaeleontidae Family of Reptilia is easily understood.

+ present a roadmap of some simpler cognitive processes related to vision involving color rendition and feature extraction--with proper emphasis given to the importance of motion in these cognitive processes.

+ provide a proposed redefinition of many theorems, postulates and hypotheses of vision with proper weight given to the corollaries associated with each of them that must be observed.

+ present a new and expanded description of a "standard human eye" for active use in furthering both teaching and research on the eye and also development of new appliances, pharmaceuticals and treatments for the eye.

+ provide a rigorous description of the dynamic characteristics of the eye with parametric simplifications explaining the overall spectral characteristics and the overall temporal characteristics of a specified animal eye.

1.3.2.3 Tools conspicuously lacking in the current VISION literature

To an outsider, the level of understanding of statistics among modern biological researchers is shocking. Many of them have not progressed beyond simple cookbooks on the normal distribution, with occasional excursions into the siblings of the normal distribution, the binomial and Poisson distributions. The log-normal distribution, which is the fundamental distribution related to growth in organisms, and the Fermi-Dirac distribution, critical to understanding the reaction of sensory materials to light photons, are not even listed in the index of most texts with titles like Statistics for Biologists[104,105]. The log-normal distribution is one of the class of exponential distributions.

The stated aim of Dytham in his opening sentence was, "to produce a statistics book with two characteristics: to assume that the reader is using a computer to analyse data and to contain absolutely no equations." While this was an introductory book, it may well be as far as many of his readers go in this area. While his basic message is excellent, "think about the statistics ***before*** you collect the data!", he does not expose his readers to the panoply of statistical situations they need to consider.

Failure to understand the role of log-normal statistics leaves the typical researcher attempting to determine the Skewness and Kurtosis of a data set relative to a normal curve when these two parameters are in fact zero with respect to the actual underlying mechanisms and distribution. The data in figure 6.3 of Dytham is clearly a log-normal distribution describing the elytra length in a population of beetles. It makes no sense to analyze this distribution in terms of a normal distribution. Analyzing the data using available statistical computer programs, and assuming a normal distribution, simply leads to wrong answers.

Failure to understand the role of Fermi-Dirac statistics in photodetection restricts the investigators ability to understand the unique properties of the chromophores of vision. This restriction applies even more strongly and particularly to the long wavelength (L–channel) of vision.

Within the current state of the biological art, any researcher that is not comfortable with the calculus and at least a first course in differential equations cannot be expected to go far. Someone with this necessary background can assuredly understand the basic equations of the various families of statistical distributions.

1.3.2.3.1 Tools of statistics equivalent to those in the behavioral & physical sciences

Statistics, being primarily a specialty of mathematics, has a long history but only a superficial applications within the field of psychophysics, and of physiology, related to vision. Pearson and colleagues were the first widely recognized investigators into the statistical parameters of data sets (ca. 1880). Their work was not integrated into biophysical experiments until much later.

An important note of Thompson[106] in 1996, of relevance to this work, is the definition of at least one "effect-size" parameter. He notes,

> "Classes of effect-sizes include standardized differences (e.g., the experimental group mean minus the control group mean, divided by the estimated population standard deviation). Alternatively, because all analyses are correlational (cf. Knapp, 1978; Thompson, 1991), variance-accounted-for effect-sizes can be computed in all studies."

Thompson[107] in 2002 presented a paper trying to rationalize the statistical parameters that could be used to set acceptable precision standards in various disciplines, and applications within those disciplines.

> "The purpose of the present review is not to argue whether statistical significance tests should be banned (cf. Schmidt & Hunter, 1997) or not banned (cf. Abelson, 1997). These various views have been repeatedly presented in the literature.

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[104]Campbell, R. (1989) Statistics for Biologists, 3rd Ed. Cambridge, Cambridge Univ Press

[105]Dytham, C. (2003) Choosing and Using Statistics: A Biologist's Guide , 2nd Ed. Oxford: Blackwell Publishing

[106]Thompson, B. (1996) AERA Editorial Policies Regarding Statistical Significance Testing: Three Suggested Reforms *Educational Researcher* vol 25(2), pp 26-30

[107]Thompson, B. (2002) "Statistical," "Practical," and "Clinical": How Many Kinds of Significance Do Counselors Need to Consider? *J Counseling Dev* vol 80, pp 64-71

> Instead, this article has three purposes. First, the article seeks to clarify the distinction between three "kinds" of significance: 'statistical,' 'practical,' and 'clinical.' Second, various indices of practical and clinical significance are briefly reviewed. Finally, it is argued that counselors should not consider only statistical significance when conducting inquiries or evaluating research reports.
>
> Practical or clinical significance, or both, will usually be relevant in most counseling research projects and should be explicitly and directly addressed. Authors should always report one or more of the indices of 'practical' or 'clinical' significance, or both. Readers should expect them. And it is argued in this article that editors should require them."

Substantiating his arguments that statistical rigor was important, Thompson quoted Boring as follows,

> "For example, in his critique of the mindless use of statistical tests titled 'Mathematical vs. Scientific Significance,' Boring (1919) argued some 80 years ago, 'The case is one of many where statistical ability, divorced from a scientific intimacy with the fundamental observations, leads nowhere' (p. 338)."

The field of education and psychological testing have adopted the term "effect-size" as an important tool accounting for the sample size in a given experiment. Thompson noted,

> "Given considerations such as these, Roger Kirk titled his Southwestern Psychological Association presidential address "Practical Significance: A Concept Whose Time Has Come." Kirk (1996) emphasized that statistical significance tests only evaluate "ordinal relationships" (e.g., whether two group standard deviations are different or one is larger than the other). He argued,
>
> > Is this any way to develop psychological theory? I think not. How far would physics have progressed if their researchers had focused on discovering [only] ordinal relationships [such as those tested by conventional null hypothesis tests]? What we want to know is the size of the difference between *A* and *B* and the error associated with our estimate; knowing *A* is greater than *B* is not enough. (p. 754)
>
> This emphasis on quantifying findings in service of evaluating the practical noteworthiness of results also is not new. For example, long ago Fisher (1925) advocated the calculation in ANOVA of the index called eta squared (or the correlation ratio). Similarly, Kelley (1935) proposed another ANOVA index of practical significance: epsilon squared. These indices have generically come to be called "effect-sizes." There are literally dozens of available choices. Various syntheses of these choices are available (cf. Kirk, 1996; Olejnik & Algina, 2000; Snyder & Lawson, 1993).
>
> Effect-sizes are particularly important because statistical tests are so heavily influenced by sample sizes."

Summarizing his goal, Thompson noted,

> "**Why Effect-size Interpretation Should Be Required**
>
> As readers know, the 1994 American Psychological Association (APA) Publication Manual incorporated an important revision "encouraging" (p. 18) authors to report effect-sizes. However, there are now 11 empirical studies of either 1 or 2 volumes of 23 different journals demonstrating that this encouragement has been ineffective (Vacha-Haase, Nilsson, Reetz, Lance, & Thompson, 2000)."

It does not appear the situation has changed since 2002 with regard to the field of vision, although a large majority of the journals in the field of education and psychology have adopted policies "requiring" that effect-sizes be reported.

In terms of the Luminous Efficiency Function of **Section 17.2.8**, and the Chrominance Diagrams of **Section 17.3**, there are no available "control group mean" or "population standard deviation" of adequate spectral precision. *The alternative is a detailed and precise theoretical model that can be treated as the control group mean with a population standard deviation of zero.* The model would contain detailed responses that include expected deviations from the ideal case that would prevent investigators from making patently false hypotheses based on their data from their small experimental group. Such a model is presented below.

1.3.2.3.2 Tools of quantum mechanics, semiconductor physics and advanced chemistry

The visual sciences have fallen far behind other disciplines in the use of the tools of semiconductor physics, liquid crystal chemistry, and the interaction of light with matter as a quantum physical process. The important area of electrolytic chemistry has also been largely ignored in the visual sciences.

It is remarkable how small a role liquid crystal chemistry has played in the analysis of visual function when it is the key feature of all biological tissue and processes. The liquid crystalline chemistry of the body leads to the introduction of new quantum physical characteristics not found in conventional chemistry of the three states, gas, liquid and solid. These are of two major types, the interrelationship between light and the absorbing material and the passage of electrons through junctions between such materials.

The absorption characteristics of the chromophores of vision are unique to their liquid crystalline configuration. This configuration also leads to anisotropic absorption that has caused great confusion in the visual literature because the parameter has not been quantified with relation to the more common isotropic absorption of the same material in dilute liquid solution.

The liquid crystalline state is also critical to the operation of the neural system. Every junction between two neurons, and certain configurations within a neuron, constitute an electrolytic semiconductor device, similar to a transistor, and known as an Activa. Recognizing this fact leads to a straightforward understanding of the operation of the neural system as a conventional electronic system (even if based on electrolytic instead of solid state semiconductor physics).

1.3.2.3.3 Electrostenolytic chemistry

An additional field, essentially overlooked in visual research, is the field of electrostenolytics. Electrical power to drive the electrolytic circuits of the neural system is derived from normal metabolic processes occurring on the surfaces of membranes. This is the regime of electrostenolytics. In vision, the electrostenolytic process involves the glutamic pathway or cycle. This cycle involves the reduction of a group of chemicals related to glutamic acid in order to provide energy. This fact accounts for the ubiquity of GARP, GABA, glycine and the glutamates on the surface of neurons throughout the neural system (See **Section 7.7**).

1.3.2.4 Tools used inadequately in the current literature

The current literature of vision is primarily based on linear algebra. There are rare excursions into the calculus. The few excursions beyond that into differential equations have generally produced questionable results. This has frequently been due to the approximations introduced to achieve tractability with those tools.

The neural system in general, including the visual modality employs very sophisticated mechanisms in a variety of areas that have not been broadly recognized by the Bioscience community. The use of quantum-mechanical processes in phototransduction have not been recognized in the past as have the sampled-data techniques used within the signaling channels. ***Most importantly, the neural system does NOT employ transcendental mathematical functions in its signal manipulations***. No academic literature could be found demonstrating the use of such functions within the neural system.

The massive 2002 text by Hung & Ciuffreda[108] is an example of the overlooking of these limitations in the development of understanding of the visual modality. While a *tour-de-force* as a pedagogical tool, it does not present realistic models of the visual system signaling circuits in at least the following respects,

• It employs the conventional circuit synthesis, or circuit realization techniques used in analog circuit theory. These techniques are typically labeled *s*-plane techniques in analog circuit realization. In a sampled-data system, involving "action potentials," such as the neural system, it is necessary to employ sampled-data analytical mathematical techniques. These techniques are typically labeled *z*-plane techniques in pulse circuit realization.

• Time delay is also a significant factor in the neural system, in addition to that introduced by sampling the analog data. The limitations on *average* velocity of neural signals must be represented in realistic circuit models of the visual system.

• The biological neural system, at least within the visual modality, does not employ transcendental mathematical techniques such as integration of even simple variables. It clearly does not employ transcendental mathematical techniques such as auto– and cross-correlation.

• There are significant limitations on the use of matrix algebra in modeling the neural system. These are nearly always omitted in the discussions involving matrix algebra. These primarily relate to the applicability of such matrices within the limits of actual circuit linearity.

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[108]Hung, G. & Ciuffreda, K. *eds*. (2002) Models of the Visual System. NY: Kluwer Academic/Plenum Publishers

The Hung & Ciuffreda text does not even address the techniques of z-plane analysis or the limitation in the use of transcendental mathematical manipulations within the neural system. Most of its models do not incorporate finite delays in the schematics.

1.3.2.4.1 Mathematical Preparation

There are a variety of areas in interpreting the visual process where investigators have failed to use adequate mathematical tools. This is especially true in processes that are complex functions of time--frequently involving multiple time constants. It is particularly apparent in dark adaptation, in describing the basic Photoexcitation/De-excitation (P/D) process, and in describing the saturation processes related to the P/D process. It has completely prevented researchers from understanding the oculomotor system of vision. To a lesser extent, it has also been a constraint on understanding the luminosity and chromaticity functions of vision.

The field of mathematics is usually taught in a hierarchal sequence. This sequence continually introduces more complex methods of problem solving. Without using sufficiently sophisticated methods, only results of limited scope can be obtained. For purposes of discussion the hierarchy of mathematics can be described as extending from:

1. algebra
2. differential calculus
3. integral calculus
4. linear differential equations (with constant coefficients and simple variables)
5. differential equations with complex variables
6. differential equations with complex variables and changing initial conditions (found in chaos theory)
7. differential equations with complex variables and changing (usually described as variable) coefficients
8. the theory of complex variables

9. *s*-plane analysis techniques (applicable to analog circuits)
10 *z*-plane analysis techniques (applicable to sampled data circuits).

Only items 1 through 3 are found within neural circuits, with integral calculus limited to integration of a simple variable as a function of time. Item 10 is needed to properly recover analog signal information projected over modulated pulse (action potential) data streams.

1.3.2.4.2 Extensive use of piecewise mathematical solutions

In place of adequate mathematical tools, many vision researchers have fallen back on simplified solutions applicable over only limited intervals (and frequently eliminating critical parameters). Multiple solutions of this type are frequently found and then described as a family showing hysteresis or other complicating mechanisms. These approaches may be useful for pedagogical purposes but are not adequate at the research level. A better approach to obtaining a satisfactory (complete) solution is to adopt the concepts of state-variable theory once it has been determined that the problem requires the use of differential equations with complex variables. This methodology can provide a more continuous, although not necessarily continuously differentiatable solution to the problem.

1.3.2.4.3 The introduction of matrix algebra into the analysis of non-linear analog circuits

The introduction of what has been labeled “Computational Neuroscience” into the study of the physiology of vision is intrinsically dangerous. In an effort to represent complex relationships in a compact form, matrix algebra concepts are often employed. However, neural systems employ a variety of non-linear concepts of limited dynamic range. For instance, the analog dynamic range of a typical amplifier, an Activa, within a neuron has an input/output relationship that is logarithmic and its input dynamic range is less than 200:1. Near the lower limit of this range, either source or internal noise frequently obscures the performance of the neural circuit. The investigator must insure that the useful dynamic range of all parameters are not exceeded when manipulated within a matrix algebra context.

1.3.2.5 The need to introduce more available engineering tools

The vision literature is handicapped at the present time by the lack of sophistication in its modeling. This is particularly apparent in the area of feedback and servomechanism design.

Being familiar with certain aspects of servomechanism theory is mandatory if one is to understand the fundamental operation of the Precision Optical Servomechanism System (POS) of the visual system, . Since the system is in fact a sampled data servo system, more advanced *z*-plane and sampled data techniques are involved in the precise mathematical description of the performance of the visual system. This is particularly true in the higher mammals.

However, a general understanding can be obtained if the reader is familiar with Type 0 and Type 1 servomechanisms.

In becoming familiar with servomechanism theory, the subtle difference between internal and external feedback should be carefully explored. This work has not found a significant application of external feedback in the entire visual system. However, the use of internal feedback is endemic to, and an important feature of the system. It is key to the operation of the modulation of analog signals onto pulse trains employing action potentials.

1.3.2.6 External feedback has been used as a crutch

External feedback has been used conceptually in the vision literature for a long time. The frequency of the appearance of feedback paths has decreased significantly in the last quarter of the 20th Century. There are a wide variety of discussions proposing external feedback between either bipolar or horizontal cells to inhibit the photoreceptors[109]. These have all derived from the idea that the neuron was a two-terminal device based on an excitable axon membrane. This concept did not provide an inverting mechanism within the neuron. Therefore, there was a need to define an inverting mechanism and external feedback appeared to offer a solution. With the recognition of the neuron and its kernal, the Activa, as three-terminal devices, this need has disappeared. The neuron is easily configured to perform a differencing function without external feedback. This function is found commonly among the horizontal, amercine and ganglion cells. In 1992, Dowling illustrated the capability in an obtuse way[110]. He showed, in a caricature, that it was necessary to apply a stimulus of opposite polarity to the body (poditic terminal) of a ganglion cell to obtain the same change in action pulse interval as achieved by a stimulus applied to the dendritic terminal. The fact is the synapses were not of opposite polarity but led to internal terminals of the Activa that were differential in character (**Section 10.8.1**).

External feedback plays no significant role in the visual process, except with regard the the servomechanism known as the Precision Optical System (aka. Auxiliary Optical System) that controls the motions of the eyes. The feedback path is completed by the light path from points in the external visual field to the retina of the eye (**Section 7.3**).

1.3.2.7 The recent appearance of "Special Editions" of well known journals

The journals relating to vision have recently begun to publish "Special Editions," focused on a variety of subjects. These typically contain a series of "reviews" that actually support and frequently provide additional data on the work of one or more particular well known authors in the subject area. Like the recent one prepared by Marshak & Martin focused on the S-channel of human vision, they seldom include any kind of system overview or block diagram putting the papers into context[111]. The Introduction prepared by these two editors concludes with a discussion of the shortcomings related to the group of papers and the overall situation related to the global subject.

1.3.2.7.1 [Reserved]

1.3.2.7.2 The Journal of Neuroscience "Special Edition" on S-channel in human vision

Marshak & Martin have recently edited a "Special Edition" of Visual Neuroscience focused on the S-channel of human vision [112]. The edition does not include any overall schematic or block diagram of the visual modality that places the eight papers into context. They conclude their introduction with the lament related to "Unanswered Questions:"

> "Hunt and Peichl raise our first big unanswered question: fi rst, the relation of S-cone topography to what may seem obvious environmental signals (the blue sky and the blue of the ocean) is still not at all clear. Some aquatic mammals lack S-cones but some do not, S-pigment coexpression can be restricted to dorsal or ventral retina in different species with similar lifestyle, and the spectral tuning of UVS and VS pigments in birds and mammals remains at best tenuously related to their ecological specializations. Second, if the primordial photoreceptors were S-cones, why do S-cones make up only a minority of receptors in extant vertebrates? The S-OFF pathways received a great deal of attention in the reviews by Crook et al. and Miyagashima et al., but this topic remains controversial. The existence of an S-OFF pathway mediated by

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[109]Yang, X-L, Tauchi, M. & Kaneko, A. (1983) Convergence of signals from red-sensitive and green-sensitive cones onto L-type external horizontal cells of the goldfish retina. *Vision Res*. vol. 23, pp 371-380

[110]Dowling, J. (1992) Neurons and Networks. Cambridge, MA: Harvard University Press. pg 106

[111]Marshak, D. & Martin, P. (2014) *Vis Neurosci* vol 31, pp 111–113

[112]Marshak, D. & Martin, P. (2014)

> S-OFF midget ganglion cells in the central retina of Old World anthropoids is supported by evidence from electron microscopy and psychophysics, but there has not yet been a direct anatomical demonstration of a link from the identified S-cones to the identified midget bipolar cells in central retina. This would be essential to convince the skeptics, who argue that there is very little, if any, evidence for an S-OFF midget pathway from recordings of neural activity in the LGN. A counter argument is that there are likely very few S-OFF midget ganglion cells compared with the other types, and they are expected to have atypical light responses because their receptive fi eld surrounds are mediated by, H2 rather than H1, horizontal cells. Many enduring mysteries remain unsolved at higher levels of processing. For example, unique hues (red, yellow, green and blue) enjoy universal use as basic color names across human societies, but cells tuned to unique hues have not been clearly identified at any stage of visual processing, and S-cone activity levels map to lime-violet percepts, not the familiar blue-yellow axis. These kinds of gulfs between color, as practiced by neuroscientists, and color as enjoyed by most humans are embarrassing but are a spur to further research."
>
> This work identifies a UV –S channel and an S–M channel as key to the Chromaticity Diagram (2016). See **Section 16.3.4**. *The analog UV–S channel might be mistaken for an S–OFF channel if the sensitivity of the retina to UV light was not recognized or accepted.*

This work does provide both a framework (block diagram and schematic of the complete visual modality) applicable to any species exhibiting vision and a new performance description regime that explains the inadequacies described by Marshak & Martin.

The first paper by Hunt and Peichl is more than controversial. It presents a free-hand set of spectral response functions lacking any data points and based on a variety of psychophysical experiments without providing any discussion of the more precise physiological experiments. The wavelength ranges specified are gross without any tolerances. The purported long wavelength spectrum is that reported by behaviourists based on a faulty mathematical interpretation and totally ignores the more precise data of Thornton in the lighting laboratory and the theoretical spectrum based on the actual physics associated with the receptor chemistry. The cladogram in figure 2 spanning the complete phylogenic tree is a unique piece of conjecture showing the lamprey eal has a wider spectral sensitivity than virtually all other species except the birds, the reptiles and the ray-finned fishes. The descriptions related to a variety of mammals appear to lack any relevance to the actual laboratory record. The suggestion that primates only employ one or at most two spectral receptors is ludicrous on its face; all thoroughly explored mammals are known to employ four spectral receptors in the UV, S, M & L segments of the visual spectrum with the individual spectra being quantified to an accuracy of ±2 nm (See **Chapters 5** & **17** of this work among others). The cladogram is based on their interpretation of the significance of specific genes in determining the spectral capability of a species. Their discussion of "Opsin coexpression" is based entirely on point studies that have only uncovered a selected set of opsins and totally ignores the fact that the actual spectral receptors (the Rhodonines) are not directly associated with the opsin as a substrate. In fact, the genes they discuss do not exhibit a direct correlation with the presence of the Rhodonine chromophores that do determine the spectral capability of the species. The genes do not code for the non-protein Rhodonines.

Hunt and Peichl appear totally unaware of the effect of the lens of the mammalian eye in limiting the overall spectral response of the large mammals in spite of the presence of a full set of all four spectral receptor types within the mammalian retina.

The Miyagishima et al paper appears to contradict the Hunt and Peichl paper to a very significant degree. It also makes bazaar comments about the difference in visual capabilities of the males and females of a single family ("Most New World primates"). Their data is not based on psychophysiological testing of spectral performance but on the treating of retinas with immunohistochemical agents reported to be selective of sensory neurons of a specific spectral sensitivity. This relationship has not been documented but is widely held within a very small community of histologists. Their discussion of the amercine cells of the retina is open to a totally different interpretation. These cells operate as analog differencing circuits (**Section 13.3**) between the different pairs of receptor channels and do not operate as mere "blue-OFF" circuits.

The other papers in the "Special Edition" will not be explored here for reasons fundamentally associated with their adoption of inadequate experimental protocols and the shortcoming highlighted by Marshak & Martin in their introductory remarks highlighted above. Lacking an adequate framework of the visual modality, like that incorporated in this work, leaves the findings of that edition out of any rational context.

1.3.2.8 The recent rise of mathematical models of vision

A great variety of mathematical models have appeared during the last twenty years. They generally fail to describe any underlying physiological model in any significant detail and rely upon pedagogical material from undergraduate

textbooks for a starting point. The recent book by Li Zhaoping is a good example of this approach[113]. He defines the visual field of each eye as incorporating a 2000 by 2000 element set of photoreceptors sampling at 25 Hz based on his 2006 paper. while the mathematical techniques employed are sophisticated, the relationship with the actual physiology of vision is almost non-existent. An example is his association of stereo vision with the visual cortex without recognizing the primary role of the LGN and the PGN in this process.

1.3.3 Interpreting chrominance information and measured signal waveforms

The vision community has suffered from the "*search image*" syndrome (**Section 1.1**) most significantly in the study of chrominance information and signaling waveforms. In general, the community has sought repeatedly to confirm the views of Young in the early 1800's that vision was fundamentally trichromatic. Still in the 19th Century, Helmholtz proposed that color involved the linear summation of individual signals[114]. These positions cannot be supported at the detailed level. Hering attempted, contemporaneously with Helmholtz, to propose that the signals were linearly differenced. This idea also falls short of the actual situation defined in detail in this work. Hering was the closest to correct, the visual modality employs the differences between logarithmic values as expressed in the New Chromaticity Diagram of **Section 17.3**. This chromaticity diagram is based on theory, correctly accounts for the spectral limitations imposed by the lens of the eye, is compatible with all results properly measured in the laboratory and provides the ultimate representation being sought by the empirically measured, *and defined*, L*A*B* and L*U*V* variants of the CIE chromaticity diagrams.

1.3.3.1 Fundamentals of color manipulations

Since the 1800's, experimenters have attempted to describe vision in terms of a linear additive process involving color signals. This was before the development of color printing. Color printing employs what is known generally as "process color." Process color is a linear subtractive process. The rules of additive color processing generally apply to illuminances (sources) and do result in a "white" light, or any other color of light, to be created by mixing three different colored lights (as observed by normal trichromats). For primarily psychophysical and cultural reasons, the different colors used are typically labeled red, green and blue or R, G, & B. This is the way a cathode ray tube or other display device generates a color picture. The rules of subtractive color assume a white light is used as a source and certain parts of the light are filtered out by absorption at a reflective surface. The result is less satisfactory than that obtained by additive color. The best results in process color are achieved when inks that have a broadband absorption spectrum and are are used that are complimentary to the additive colors of R, G, & B. These colors are known as Cyan, Magenta and Yellow, C, M, & Y.

It will be shown that the visual system in animals does not employ just linear additive processing or just linear subtractive processing. It will also be shown that the visual system treats the luminance information and the chrominance information in fundamentally different ways. The initial signal detection channels employ chromophores that do not correspond to the conventional R, G, & B. They are designated more accurately by UV, S, M, and L in vision. Humans and other large chordates cannot use the UV channel effectively. The three or four detection channels are summed in logarithmic space to create the brightness information transmitted to the brain. The same three or four detection channels are differenced *in pairs* in logarithmic signal space. The result is two or three parallel chrominance signals representing the ratio of the chrominance components. The resulting three or four signaling channels, one brightness and two or three chrominance channels, are transmitted to the brain for further processing.
The important point is that the visual system does not employ and should not be modeled as employing either linear additive color or linear subtractive color. The results obtained will be inappropriate or irrelevant and the conclusions drawn will be misleading.

1.3.3.2 Fundamental chromatic classes of eyes

Except for some of the simplest eyes found in *Arthropoda*, the known animal eyes are multi-spectral and employ some degree of initial signal processing to obtain chromatic information. This processing is usually within the retina or near the retinula. The filtering may involve only a small group of cells in a retinula sharing a small area of the focal plane behind a simple lens. Alternately, it may involve a large mosaic of cells forming an extended retina behind a very sophisticated optical system. In either case, the total incident light is distributed between the different chromatic photodetectors in the focal plane.

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[113]Zhaoping, L. (2014) Understanding Vision: theory, models, and data. NY: Oxford Univ Press

[114]http://poseidon.sunyopt.edu/BackusLab/Helmholtz/ (A JOSA reprint of Southall's 1924 translation of Helmholtz's original 1910 treatise.

The literature has many references, frequently based on human egocentricity, to the color capabilities of the visual systems of different animals. Most of these references support the assumption that the human eye is the most advanced chromatically. In the more egocentric literature preceding the 1980's, only man and a few primates enjoyed color vision. In fact, the human eye, and that of all other large chordates, is more limited chromatically than most animal eyes. The fundamental architecture of the visual system provides for four chromatically different photosensing processes with peak spectral sensitivities equally spaced across the "visual spectrum," within the range of 300 and 700 nm. The term "visual spectrum" is in quotation marks because the human visual spectrum, in practice, only extends from 400 to 700 nm. This is due to the lens group, the cornea and lens, and not because of a limitation in the retina. The human retina is known to contain all four of the potential chromophores. In the absence of the lens-group, the retina shows a higher ultraviolet range than it does in the blue.

Looking at the visual phylogenic tree in total, there appear to be four different classes of eyes based on their chromatic capability. The most general type is the complex, tetrachromatic, eye found in *Mollusca* and *Chordata*. In this eye, the retina is a mosaic of all four types of chromatically specific photodetectors. It offers the widest possible spectral range. In the large chordates, the cornea-lens group does not transmit ultraviolet light well and the UV sensitive features of the retina are degenerate or unused. The resulting long wave trichromatic class of eyes is the second type. Interestingly, the aphakic human eye is ultraviolet sensitive as mentioned above. For reasons that appear to be related to temperature during gestation, Arthropoda frequently exhibit a different class of chromatically capable eyes. This third class of eyes is trichromatic but sensitive to the short wave triad of the available spectral ranges, the UV-, S-, & M -. It is commonly found in the compound eye of the insects. The fourth chromatically defined class of eyes is found in the simple eye or ocellus of Arthropoda. This eye is frequently reported to only exhibit a limited spectral range based on the UV- sensitive photodetector, sometimes the UV- and S-sensitive photodetectors.

There are many references in the literature to eyes exhibiting only a single pigment system. Many of these are accompanied by a spectrogram. Most of them are in error due to the limited understanding of the visual system on the part of the investigator and/or the limitations of the spectrograph. A vast majority of these spectograms exhibit a characteristic very similar to that of humans, even exhibiting selective spectral adaptation[115]. Many of them have been fitted to Dartnall nomograms that are clearly based on trichromatic vision. The measured spectrogram is usually the smoothed composite brightness response of the animal.

Menzel writes in 1979 that "A mollusc eye containing more than one photopigment has yet to be found." He then goes on to discuss a nudibranch with a "single photopigment" with a peak absorption at 500 nm. and the fact that *Pecten maximus* has two separate spectral maximums at 540 and 475 nm[116]. The first is clearly a normal scotopic luminance spectrum of a trichromat. The second is almost surely a normal trichromat under photopic conditions with a possible Brezold-Brucke peak at 495 nm averaged with a S-channel peak at 437 nm and smoothed to give a 475 nm peak.

The Minke paper appears to show spectral peaks at 437 and 532 nm and a distinct Brezold-Brucke peak at 494 nm. However, the filters used by those authors were less than adequate in spacing and their light source was at a low color temperature.

There are many egocentric based discussions of the extent of color vision within the phylogy versus time period. In this regard, any discussion should reference the paper of Burkhardt, et. al[117]. They show that a very ancient fish exhibits the same three chromophores as current fish and other animals. They give the peak wavelengths as 457 ± 5nm, 556 ± 2 nm and 624 ± 6 nm in a fish known to be at least 400 million years old. While it can be argued that the animal could not perceive color, the mechanisms are clearly present to accomplish this.

1.3.3.3 Commonality of chromophores throughout the kingdom

In the 1960's, a wide range of peak spectral sensitivities were reported for different animals. The values reported almost represented a continuum. More recently, laboratory technique has improved and the reported spectral peaks have begun to converge into four regions, 325-350, 425-450,525-550 & 600-625 nm. Gouras has provided a recent

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[115]Minke, B. Hochstein, S. & Hillman, P. (1973) Early receptor potential evidence for the existence of two thermally stable states in the barnacle visual pigment. J. Gen. Physiol. vol. 62, pp 87-103

[116]Menzel, R. (1979) *in* Comparative physiology and evolution of vision in invertebrates, A: Invertebrate photoreceptors, Autrum, H. *Ed*. NY: Springer-Verlag, pg.540

[117]Burkhardt, D. et. al. (1983) Cellular mechanisms for color-coding in holostean retinas and the evolution of color vision. *Vision Res*. vol. 23, no. 10, pp 1031-1041

compilation[118]. A glaring exception is for the human where many reports still place the peak sensitivity of the long wavelength photoreceptor near 560-570. This is primarily due to conceptual errors in experimental design which will be explored in depth later. Based on this model, the peak sensitivities of the visual chromophores, with little chromatic difference due to temperature or other environmental factors, are 342, 437, 532 & 625 nm. ± 2 nm. The spacing is significant. The wavelength is directly related to the order of conjugation of the underlying chromophores.

1.3.3.4 Commonality in the spectra of color vision

Chapter 5, and particularly Section 5.5.10 will show that the above wavelengths are the center wavelengths of the chromophores of vision, the Rhodonines. The width of each of the spectral channels varies slightly as a function of the configuration of the outer segments of the photoreceptor cells. **Figure 1.3.3-1** shows the center wavelengths and typical spectral widths of the four spectral channels of biological vision.

It remains an early day in determining the spectral capability of animals, in all phyla. However, it is rapidly becoming apparent that the basic architecture of biological vision is tetrachromatic. Individual species are frequently found to be trichromatic for a variety of reasons. The principle reasons lead to two groups, A large number of short wave trichromats, UV–, S– & M– sensitive, among large families of *Arthropoda*, and a large group of families described as long wavelength trichromats, S–, M– and L– sensitive, among the physically large members of Chordata. This latter group includes man. However, the retina of man is actually tetrachromatic as discussed below.

Progress in determining the complete spectral capability of species has been slow because of the techniques and protocols that have been found most convenient. Many of these collect data on the spectral responses of an ensemble of photoreceptors, frequently without introducing or controlling the state of adaptation in the individual spectral channels. This is frequently performed using ERG or LERG techniques. When using LERG techniques, the tendency is to investigate signals related to the luminance channel. The signals collected in this way exhibit the summing of logarithmic signals. The result is a spectrum that favors the most sensitive channel to the near exclusion of other channels. In this case, the shoulders in the composite waveform are frequently the only indication of the presence of an underlying spectral channel absorber.

Arthropoda has been known to be sensitive to ultraviolet light since 1914. There is considerable data showing they are sensitive to the S– and M–channels of vision. The recent experiments of Eguchi, et. al, have shown a significant sensitivity to even longer wavelengths, the L–channel, in this phylum[119]. In some of their recordings, the L–channel is represented by a clear peak (figure 3). In others, its presence is suggested by a shoulder (figure 1 & 2). Their test set did not extend far enough into the UV to give clear results. However, this area has been explored extensively by Goldsmith and others (See Section 3.6.1).

The vast majority of *Chordata* (*Vertabrata*) are known to be tetrachromatic. Their eyes sense light in all four of these spectral channels. Unfortunately, the large chordates, including man, have a lens that absorbs ultraviolet light. Although their retina is tetrachromatic, the overall system can be described as a long wavelength trichromat, shown in **Section 17.3.3**. It is a blocked tetrachromat because of the lens.

The research is incomplete with regard to *Mollusca*. It is known that they use the two middle spectral channels. However, only behavioral evidence is available to show they use the long wavelength spectral channel.

In each of the above cases, the brightness sensitivity of the animal is described by the logarithmic sum of the appropriate channels (after introduction of a weighting function). Because of the logarithmic mechanism, the

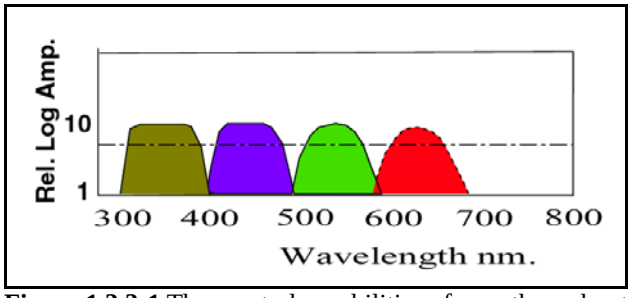

Figure 1.3.3-1 The spectral capabilities of eyes throughout the animal kingdom. It is well documented that *Arthropoda* employs the left three spectral channels and *Chordata* uses all four (with the exception of the large chordates like man) The large chordates use only the right three colors because of absorption of the ultraviolet by their lens. Research has confirmed that *Mollusca* uses the two middle spectral channels. It probably uses the right most channel as well.

[118]Gouras, P. (1991) The perception of colour, vol.6 *in* Vision and visual dysfuncton. Boca Raton, FL: CRC Press pg. 73

[119]Eguchi, E. et. al. (1982) A comparison of electrophysiologically determined spectral responses in 35 species of *Lepidoptera*. *J. Insect. Physiol*. vol. 28, no. 8, pp 675-682

visibility functions of many animals show auxiliary peaks that are not present in the individual spectral characteristics. This is particularly true for humans where the normal photopic peak is near 555 nm. The peak under scotopic conditions is found at 494 nm because the long wavelength channel is not functional at low light levels. The above values are a function of the test conditions used to measure them. Additional peaks are frequently introduced under abnormal conditions. These mechanisms are discussed in detail in **Section 17.2.2** and the equations of **Section 16.3**.

1.3.3.5 Universality of color vision over time

Many physiologists and anthropologists have speculated on the evolution of color vision. They have generally proposed the recent achievement of color vision among the higher primates. There is no foundation for these speculations. The oldest known members of the fossil record, and the most primitive living species, had or have the physiological capability for achieving color vision. *Limulus*, an archaic member of a minor branch of *Arthropoda*, *Chelicerata*, is still with us today as are many members of *Planaria*. *Limulus* is interesting in that it has a simple, dorsal ocellus that appears to be sensitive to all four of the spectral bands of the visual spectrum. Although discussed in terms of two separate chromatic channels by Lall[120] based on the measurements of Chapman & Lall, the data presented to describe the long wavelength channel is clearly indicative of the normal tetrachromatic eye. It has a spectral range of 300 nm to 650 nm as measured at 1% of peak amplitude and displays a luminosity function common to the tetrachromatic class of eye. Animals virtually identical to the present day *Limulus* were in existence 180 million years ago. It obviously evolved during an earlier period.

1.3.4 Necessity of scientific rigor when conceiving an experiment

In reviewing the literature, one of the most obvious problems is the pervasive lack of good experiment design in the conceptualization of an experiment. This is primarily associated with lack of adequate parameter control. By planning an experiment without the benefit of a comprehensive overall model of the system being studied, knowing what parameters must be controlled is difficult. Similarly, an experiment planned without a thorough knowledge of the possible outcomes frequently leads to a conclusion that is too narrowly drawn based on the facts. The experimenter tends to confirm his "search image" as discussed in **Section 1.1**.

Finding any attempt in the literature to recognize, separate and account for the metabolic aspects versus the signal generation and transmission aspects of cell performance is rare.

The era of exploratory experiments where an accuracy of an order of magnitude, or one-half an order of magnitude, is sufficient is long passed. Even in biology, accuracies of at least +/- 10% are now required (even if only to establish the mean) and accuracies of +/-5% are usually obtainable with careful experimental design and implementation based on a good underlying conceptual model. Such accuracies involve careful statistical as well as physical design of experiments. To achieve such accuracies representative of a process or mechanism associated with a species or family, using more than one specimen is necessary.

The accuracies described above require careful documentation of the *in-vitro* or modified *in-vivo* conditions involved if traceability to the general *in-vivo* case is to be maintained.

1.3.4.1 Defining a hypothesis clearly

Few references to "the scientific method" appear in the literature of vision. Still fewer papers indicate compliance with this method of investigation. Frequently, the methods section of a paper is limited to the mechanics of handling the specimen. This does not provide a comprehensive description of the experiment. In psychophysics particularly, it is common merely to list the manufacturers model number associated with some instrumentation rather than define the parameters involved in the experiment and the accuracy to which they were determined or controlled. This approach is entirely unacceptable within the scientific method.

The experimental method requires a clear exposition concerning what is expected and why. Uttal presents a valuable discussion of the traps that an experimenter can fall into through lack of adequate preparation of his initial thesis[121].

1.3.4.1.1 Insufficient parameter control

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[120]Lall, A. (1970) Spectral sensitivity of intracellular responses from visual cells in median ocellus of *Limulus Polyph*. Vision Res. Vol. 10, pp. 905-909

[121]Uttal, R. (1981) A taxonomy of visual processes. Hillsdale, NJ: Lawrence Erlbaum Associates. pp. 741-743

As will be seen later, a good example of insufficient parameter control concerns measurements of the spatial or temporal frequency response of the human eye. Many reports are in the literature concerning this subject. However, reconciling the various data is very difficult because the authors did not realize the importance of controlling several parameters in their experiments. They generally did not realize that the temporal response of the various photoreceptor channels is a direct function of the illumination level employed. Furthermore, as shown later, the investigators did not recognize that the data they obtained, which was collected following at least one computational step within the retina, represented a difference signal between two photoreceptor channels. These channels exhibited different net gains at that point. This caused the data to be highly dependent on the chromatic characteristics of the input signal, which were not controlled or specified in the report, a clear case of a "floating model" to be discussed below.

1.3.4.2 Poorly designed experiments

Moon & Spencer made a number of interesting observations concerning vision research[122]. "The fundamental assumption that must be made in all visual theory is that a complicated organism will give reproducible results which can be approximated by mathematical expressions. to anyone who has noted the erratic fluctuations obtained from day to day in visual tests, this basic assumption is disquieting. But it must be made if anything is to be accomplished in visual theory."

Based on more recent work, it is clear that much of the variability in psychophysical experiments in particular, is due to inadequate control of variables during development of the protocol. Much data is reported in the literature that should only be used to plan more precise follow-on experiments.

Based on the current state of the art, it is no longer creditable to claim the visual system is linear. Nor is it productive to plan any experimental protocol based on that assumption.

1.3.4.2.1 Matching the illuminants to the chromophores

Probably the most common, and continuing, shortfall in experiment design is assuming that the illuminants used only affect the desired chrominance channels. To insure the minimum confusion in the data, narrow band illuminant sources should be used. These should be selected to maximize the light applied to the desired chrominance channel and minimize the light applied to the other chrominance channels. This is a straightforward process based on the spectra presented later in this work. The important point to recognize is that the significant overlap between the M-channel and the L-channel frequently found in the literature is due to a problem in experiment design. It is well documented that the L-channel peak response is near 625 nm. The value of 575 nm, frequently found in the psychophysical literature, is obtained for one of several reasons. Frequently an action spectrum is computed based on the C.I.E. photopic luminosity function. Occasionally, an action spectrum is computed based on inadequate chromatic adaptation. Generally the spectrum is computed based on an assumption of linearity. Frequently, the subject was given inadequate instructions on how to avoid responding to a luminance peak when a chrominance spectrum was being investigated. Framing such an instruction may not be possible. Conversely, it may not be possible for the subject to perform based on such an instruction. The 575 nm. peak in the achromatic spectrum of human vision is an artifact of the signal processing algorithm under conditions of spectral adaptation.

Off optical axis experiments are particularly difficult to design because of the amount of computation performed in the retina and/or the cortex. If the computational matrix is not known, the experimental results may exhibit properties related to the three spheres of such processing, brightness, chrominance and appearance, in an uncontrolled and/or unexpected manner.

1.3.4.2.2 Inadequately specific chemical tests

When carefully reading the vision literature, one frequently encounters authors drawing a specific conclusion from a nonspecific test. When dealing with complex organic chemicals, this is frequently not justified. Stating that a material is such and such because it reacted in such a way with a given chemical is common. This is frequently a definitive test when a reaction occurs after mixing simple chemicals. However, with complex molecules, it is at best an indication of possible presence of a given species. The actual material may be a member of a family that all give the same result for a given test. It is important that the experimenter limit his extrapolations to what the possible results are. This is particularly true concerning the retinoids; the family is very large and many materials will give positive results with simple tests. Some retinoids will test positive for both the alcohol, retinol, and the aldehyde, retinal, because they contain both functional groups. The Carr-Price Method is particularly dangerous in this regard.

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[122]Moon, P. & Spencer, D. (1943) The specification of foveal adaptation *J Opt Soc Am* vol 33(8), pp 444-456

1.3.4.2.3 Planning and performing center-surround experiments

This work does not include discussions of center-surround experiments. **Section 15.2.4** will briefly discuss the psychophysical experiments reported in the literature. They do not include any schematics of the neural circuits involved within the visual modality.

Although center-surround experiments are easy to design at a cursory level and easy to implement in a psychophysical laboratory, they suffer from very fundamental theoretical problems. These problems lead to interesting data within a small data set but to inherently contradictory data when examined in the context of a larger data set. They are all based on the fundamental premise that the visual system employs an imaging type of detector as opposed to a change detector. Based on this intrinsic assumption, they assume that the absolute value of a stimulus is recorded by the individual photoreceptors and that these values are manipulated within the signal processing portions of the system even if their point of origin is separated by significant distances. The implication is that all of the photoreceptors in a given area exposed to the same intensity and color of light inform the signal processing system that they are receiving the same intensity and color of light. This is not true.

The above fundamental premises and assumptions are not applicable to the visual system. First, the visual system does not employ an imaging sensor. Each photoreceptor of the retina is a true change detection sensor. Second, because of their internal adaptation amplifiers, the individual photoreceptors of the retina exhibit negligible ability to generate an output signal amplitude that is directly proportional to its input. Third, the basic signaling architecture of vision does not preserve chromatic information on a pixel by pixel basis. The visual system extracts the chromatic content of the pixels in a scene on each side of a border representing a change in luminance contrast and transmits this information to the brain. The brain recreates its best estimate of the chromatic content of the scene by connecting the dots of constant (relative) illumination to create contours. It then uses a “Paint” program to fill in the nominal color within each contour based on its best estimate of the correct value. The validity of these statements is well documented by the work of Yarbus and of Ditchburn and the fact they have been incorporated into the basic color television standards used all over the world. An additional consideration is that the signals from the foveola are not processed within the same signaling channels as the rest of the retina. This makes the diameter of the center and the surround, relative to the diameter of the foveola, important parameters in the overall experiments. The variation in the transient performance of the individual signaling channels adds additional parameters to the overall experiments that must be either controlled or recorded. The experimental challenges with this type of experimentation will be addressed further in **Chapter 15**.

1.3.4.3 Poor choice of stimulus

Vision investigators as a group have not adequately specified and controlled the light stimuli used in their experiments. The problem has three aspects.

+ poor choice of the color temperature of the source used in wide spectral bandwidth experiments.

+ poor choice of broadband filters used in color recognition experiments.

+ use of excessively wide spectral filters when determining the luminosity function of the overall visual response

The color temperatures of sources commonly used in laboratory experiments do not provide equal excitation of each chromophoric channel. This has been a problem dating from the 1800's when it was generally assumed that a light source exhibiting an equal energy per unit wavelength spectrum would be most appropriate. It was assumed that such a source would stimulate each visual chromophore equally. It was also assumed that fixed spectral bandwidth narrow band filters could be used between the source and the subject to generate equal intensity excitation of each chromophoric channel. These assumptions were all based on the underlying assumption that the visual chromophores were energy sensitive devices. The fact is they are photon flux sensitive devices. There are a lot fewer photons per unit energy at short visual wavelengths than there are at long wavelengths. The lower amplitude of the signals in the S-channel under equal energy illumination accounts for the frequent comment by the electro-physiologist that an S-channel signal or an S-channel photoreceptor could not be located. The problem is further compounded by their frequent use of low color temperature light sources.

Rodieck has addressed the subject of equal flux versus equal energy spectrums using an interesting analogy[123]. If you want to heat (burn) the retina base your work on energy. If you want to excite the photoreceptors, base your work on photon flux. He also points out that the peak in the luminosity function changes between energy-based and flux-based presentations. His most recent work introduces a more radical perspective. He adopts the use of

[123]Rodieck, R. (1998) Op. Cit. Pg. 513-515

frequency instead of wavelength in working with radiation. He does this based on the observation that the wavelength is a function of the dielectric constant of the material the radiation is passing through whereas the frequency is independent of the host material. The statement is true but it may not warrant the conversion of the entire visual science to one based on frequency. Some of his justification is less true. In particular, he says: "In fact, when speaking about the interactions of light with matter, *actual* wavelengths are never used. Instead, a *defined* wavelength is used, equal to the wavelength that light would have if it were in a vacuum." In this work, the interaction of light with the chromophores of vision is discussed in terms of the actual wavelength of the light within the chromophores. Similarly in optical design and ray tracing, the wavelength and the index of refraction, as a function of wavelength, are critically important parameters. Interference effects are much easier to understand based on the wavelength parameter. Furthermore, the high efficiency of the Outer Segment of the photoreceptors is critically dependent on the variation in the index of refraction of the host materials.

Table 1.3.3.4 illustrates the relative number of photons present in a narrowband spectral range at the peak wavelengths of the visual chromophores as a function of color temperature. The color temperature is of a black body source (approximated by a filament type light source).

TABLE 1.3.3.4
Relative photon flux per unit bandwidth of a black body source

Color Temp.		**Wavelength in nanometers**			**Range**	
Kelvin	**342**	**437**	**532**	**625**	**%**	**λ**
2780	-0.974	**-0.735**	**0**	**+1.263**	+/-100,	S-L
5500	-0.621	**-0.249**	**0**	**+0.101**	+/-17,	S-L
6000	-0.526	**-0.181**	**0**	**+0.037**	+/-11,	S-L
7053	-0.317	**-0.057**	**0**	**-0.057**	+/-5.7,	S-L
8073	**-0.116**	**+0.041**	**0**	**-0.118**	+/-7.9,	UV-L
8683	**0**	**+0.091**	**0**	-0.145	+/-5.0,	UV-M

This table shows that for a 5500 Kelvin blackbody source, the photon flux applied to the S-channel (437 nm) chromophore is down a factor of 0.249, or 25% from the flux applied to the M-channel chromophore. Over the range from the S- to the L-channel, the amplitude variation is +/-17.5%, hardly an equal excitation situation. The bold figures in the table show the range used to calculate the amplitude variation shown on the right. This range is also shown in the right-hand column. The nearest the experimenter can come to equal excitation per unit bandwidth for the trichromatic spectrum using a blackbody source is seen to be +/-5.7% at a color temperature of 7053 Kelvin. More precise control of the flux density would require additional shaping of the radiant intensity or adjustment of the filter width at each center frequency. The last two lines show that the best color temperature for observing the visual response of UV sensitive animals is either 8073 or 8683 Kelvin depending on the overall range of interest.

Investigators have frequently employed spectral filters with passbands that were not chosen with proper regard to the spectral absorption wavelengths of the individual chromophores. This has led to contamination of much of the data due to uncontrolled absorption by the various photoreceptors. Unfortunately, a "green filter," using the colloquial name, excites both the S-channel and M-channel chromophores.

The determination of the spectral characteristics of the individual chromophores, and the overall luminosity function of humans, has usually employed filters of inadequate selectivity. With the half-amplitude spectral width of each chromophore equal to 70 +/-5 nm, using narrowband filters wider than 10 nm to determine the detailed spectral response of an individual chromophore is inappropriate. A similar filter width is also necessary if adequate measurement of the actual luminosity function is to be obtained, including the local minima and maxima in that function. The presence and amplitude of some of these minima and maxima depend on the stimulus level. Without recording these features in detail, supporting an accurate theory of the luminosity function is impossible.

1.3.4.3.1 Controlling the experimental interfaces

When performing neurological experiments *in-vitro* or through invasive procedures that may affect the environment of the tissue under test, it is essential that all interfaces be controlled. This applies to not only the input and output conditions but also the "supporting" conditions. Hodgkin and Huxley stressed how important it was to remove all input circuitry (dendritic material)from the axon before attempting to experiment with it. This precaution insures stable measurements associated with the axon tissue but destroys the Activa and precludes any measurements describing the complete neuron.

If a complete neuron is to be studied, the input and output circuits must be stabilized. Stabilization does not imply

the circuits must be removed, for this will destroy the biological transistor at the heart of the neuron. Stabilization of the input circuit(s) means the voltages and currents applied to these elements must be held constant or varied in a planned manner.

For the output of the axon, several considerations are important. If the axon is disconnected from all orthodromic dendritic elements, it must be realized that the circuit is now operating without an external load, i.e., in an open circuit mode with respect to the load. If it is disconnected from all antidromic dendritic elements, or these elements are destroyed, the axon is no longer in an operational condition.

If the axon is washed, it will also be disconnected from its internal load and its power source, consisting of both the load diode and the supply battery. If the entire neuron is washed, the circuitry associated with all three of the terminals of the axon will be disturbed. For a neuron to operate, it must be surrounded by an electrolyte of the proper impedance and be coated with the appropriate metabolic chemicals to support local electrical power generation. The electrolyte provides current paths for both the signal and bias circuits. The metabolites provide the necessary electrical potentials. Thus placing an unwashed neuron in a saline solution and oxygenating the solution will extend the operating life of the neuron until the metabolites are exhausted at one or more terminals. If the appropriate metabolites are also provided, the neuron will remain viable much longer.

Precautions similar to the above apply to psychophysical experiments. Any dim red light used during these tests will affect the achromatic, and most chromatic, test results since the L-channel chromophore will be affected. The presence of such a light must be documented and hopefully quantified.

1.3.4.4 Poor choice of supporting instrumentation

1.3.4.4.1 Probe techniques

When an external electrical probe is used to test a neurological circuit, it must be recognized that for retinal circuits, the impedance of the probe is usually lower than the circuit impedance. Most of the circuits of the retina are sensitive to the capacitance present relative to the resistive impedance. If the probe capacitance is too high, the circuit will oscillate; it will produce abnormal “action potentials” no matter what its normal function. This can also occur if the metabolites near the poda terminal are affected.

Most man-made probes still exceed the size of the neurological elements of the retina. Therefore, the introduction of such a probe normally involves contacting multiple retinal elements or the sensing of a zone of electrolyte that may be in contact with several OS or IS structures. The measurement may exhibit the characteristics of this electrolyte and not those of a specific neurological element. This is a particular problem since a signal recorded in this way may emulate (imprecisely) the signal summation circuits found in the cortex of the brain but not in the retina.

The use of a coaxial probe offers interesting possibilities related to invasive probes, but the size of the probes is still critical. The outer probe clearly contacts a significant volume (area) of material and the internal probe is probably still larger than desired.

It is extremely important to know where the probe is and what it contacts during measurements. The spatial accuracy desired is at the micron level for precision work. This is a clearly difficult objective when dealing with soft tissue with no mechanical reference surfaces. Some optical techniques associated with boroscopy may be adaptable while dye injection techniques are clearly better than nothing.

1.3.4.4.2 Signal Summation techniques

While the signal summation resulting from an oversize probe may be inconvenient, the use of a broad-area electrically conductive patch such as in an ERG involves signal summation by definition. These techniques are excellent at measuring signals due to poor return circuit conductivity; they are virtually useless for measuring individual circuit performance. In the typical ERG, the waveform recorded is a summation of all of the electrical signals associated with the overall retina. It is especially important to understand and control both the intensity and the chromatic content of the illumination environment in ERG experiments. This is virtually the only method of interface control available to the investigator. This control must also include the parameter of time as it affects the state of adaptation of the eye. Note, the LERG is not a true ERG involving an external summation contact but an invasive probe technique usually contacting an electrolytic reservoir.

1.3.4.4.3 Adequate performance in the spectral measurement equipment

A large number of the spectral measurements reported in the literature were acquired with inadequate spectrometers.

This can profoundly affect the experimental results obtained as shown in **Figure 1.3.4-1** from Wolken. The caption was transcribed exactly. He shows two spectra of a chromophore from a frog. The differences are startling. The two spectra taken with spectrometers of 30 nm and 5 nm resolution are hardly comparable. He gives little detail but it appears the two waveforms have been scaled since **(b)** cannot be positioned correctly if it was to be represented by **(a)** when smoothed by a 30 nm. filter. There is virtually no detail in the 30 nm. recording. A spectrometer with a bandwidth of less than or equal to 5 nm. is necessary for modern laboratory work.

More recently, there has been a movement toward using stock color monitors for purposes of psychophysical experiments without recognizing or defining the characteristics of these devices. The assumption being that all of these monitors use the same phosphors to generate light, are perfectly aligned internally to provide spectrally uniform chromatic output over a significant portion of their screen. Some investigators introduce signals directly to the grids of the cathode ray tube under the assumption that the monitors exhibit a fixed gamma regardless of the electrical input terminals used.

These assumptions are generally not valid. Even the European standards for the phosphors to be used in commercial televison differ from those for the United States. Cowan & Rowell have summarized the experimental considerations that must be addressed before using monitors in color vision research[124,125].

There is a general tendency to describe a light source by its wattage. This is an entirely inappropriate parameter. The requirement is to know its luminance and its color temperature. Pokorny, et. al. provide a comprehensive discussion of illuminants for use in psychophysical experiments[126].

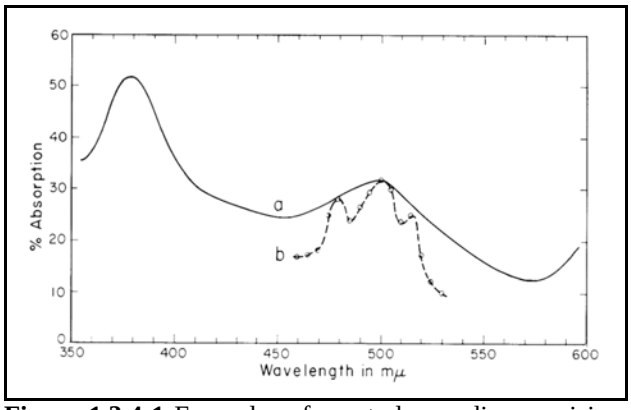

Figure 1.3.4-1 Examples of spectral recording precision. (a) Absorption spectrum of frog rhodopsin at unspecified spectral resolution. (b) Absorption spectrum at 5 mμ intervals from 460 to 530 mμ. From Wolken (1966)

1.3.4.5 Lack of attention to the statistical parameters associated with the results

Research and applications related to vision have long ignored the statistical requirements on the data used to quantify the accuracy of the data upon which hypotheses are based and decisions on future directions to be taken in the field. These requirements have frequently been deprecated based on the limited group of cohorts available to the investigator. In this situation, it is even more important to explicitly note the size of the cohort used in the final data collection along with an expression of the accuracy of the data, frequently an R^2 or *p* value that must be associated with a cohort size, or other dimension.

Statistics, being primarily a specialty of mathematics, has a long history but only a superficial applications within the field of psychophysics, and of physiology, related to vision. Neyman and Pearson were the first widely recognized investigators into the statistical parameters of data sets (ca. 1880). Their work was not integrated into psychophysical experiments (primarily involving pedagogy) until at least the 1980's (one hundred years later).

Pearson, who led one major school of statisticians[127] for one-half century or more, closely associating his "closeness of fit" with the χ^2 test, using the expression "*P*, χ^2 test" to describe the total concept. He also defined the term *graduation* throughout his discussion to connote a fitted mathematical model for the observed data. In the common case of data supposed to have been obtained from a continuous distribution, *the graduation curve is the estimated distribution curve or density*. In 1935, Pearson wrote a long defense of his approach to statistically evaluating the fit of a proposed hypothetical curve to the actual curve,

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[124]Cowan, W. (1983) Computer Graphics, vol. 17, pg. 315
[125]Cowan, W. & Rowell, N. (1986) Color Res. Appl. vol. 11, S34
[126]Pokorny, J. Smith, V. Verriest, G. & Pinckers, A. (1979) Congenital and acquired color vision defects. NY: Grune & Stratton pp. 101-106
[127]Inman, H. (1994) Karl Pearson and R. A. Fisher on Statistical Tests: A 1935 Exchange From Nature *Am Statistician* vol 48(1), pp 2-11

> "I introduced the *P*, χ^2 test to enable a scientific worker to ascertain whether a curve by which he was graduating observations was a reasonable 'fit'. On this account, and as a measure of success in graduation, I termed it a 'goodness of fit' test. It had no special relation to the normal curve or to any other curve. The scientific worker in the past had chosen any curve he pleased to graduate his observations, but he rarely applied any measure of its aptness, beyond looking at a graph to 'see' whether it was a 'good fit'. The pages of the Royal Society *Transactions* and *Proceedings* are evidence enough of this fact."

Inman closed his analysis of the two schools of statistics in 1935 with the assertion,

"Buchanan-Wollaston[128] argued that the result of some statistical test still served a limited scientific purpose when it proved to be non significant in the statistical sense. Unlike Fisher, Buchanan-Wollaston did not want to ignore sample outcomes that did not attain statistical significance. Unlike Karl Pearson, Buchanan- Wollaston was reluctant to banish the search for truth from the scientific enterprise. The apparent conflict between the objectives of statistical tests and scientific inference prompted Buchanan-Wollaston's appeal to Pearson and Fisher. Despite occasional assertions that statistical inference and scientific inference are identical, this conundrum still continues to shape the dialogue between statisticians and scientists."

Thompson[129] in 1996 presented an important paper relating to the use of statistics within the behavioral sciences that portended the changes he reviews in the following 2002 paper. After discussing the difficulty of computing *p*-values prior to the computer age, he notes,

> "Unfortunately, very few researchers seem to understand what their p calculated values actually evaluate (Carver, 1978). Put succinctly, $p_{CALCULATED}$ is the probability (0 to 1.0) of the sample statistics, ***given the sample size***, and assuming the sample was derived from a population in which the null hypothesis (H_0) is exactly true (Thompson, 1994a). The computation of $p_{CALCULATED}$ in a particular study includes consideration of three elements:
> (a) the results in the sample (i.e., the sample "statistics") vis-a-vis the null hypothesis (i.e., sample means, medians, standard deviations, or whatever a given null hypothesis is about);
> (b) the related results in the population (i.e., the population "parameters") vis-a-vis the null hypothesis (i.e., population means, medians, standard deviations, or whatever a given null hypothesis is about); and
> (c) ***the sample size***."

> "But why must computations of $p_{CALCULATED}$ take into account the researcher's ***sample size***? The answer is that sample statistics other than those that exactly honor the null hypothesis are less and less likely (i.e., yield smaller and smaller $p_{CALCULATED}$ values) as the sample size increases."

An important note of Thompson, of relevance to this work is the definition of at least one "effect-size." He notes,

> "Classes of effect-sizes include standardized differences (e.g., the experimental group mean minus the control group mean, divided by the estimated population standard deviation). Alternatively, because all analyses are correlational (cf. Knapp, 1978; Thompson, 1991), variance-accounted-for effect-sizes can be computed in all studies."

In terms of the Luminous Efficiency Function, there is no available "control group mean" or "population standard deviation." *The alternative is a detailed and precise theoretical model that can be treated as the control group mean with a population standard deviation of zero.*

Thompson[130] in 2002 presented a paper trying to rationalize the statistical parameters that could be used to set acceptable precision standards in various disciplines, and applications within those disciplines.

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[128]Buchanan-Wollaston, H. (1935b), "The Philosophic Basis of Statistical Analysis," *J Internat Council Exploration Sea*, vol 10, pp 249-263.
[129]Thompson, B. (1996) AERA Editorial Policies Regarding Statistical Significance Testing: Three Suggested Reforms *Educational Researcher* vol 25(2), pp 26-30
[130]Thompson, B. (2002) "Statistical," "Practical," and "Clinical": How Many Kinds of Significance Do Counselors Need to Consider? *J Counseling Dev* vol 80, pp 64-71

> "The purpose of the present review is not to argue whether statistical significance tests should be banned (cf. Schmidt & Hunter, 1997) or not banned (cf. Abelson, 1997). These various views have been repeatedly presented in the literature.
>
> Instead, this article has three purposes. First, the article seeks to clarify the distinction between three "kinds" of significance: 'statistical,' 'practical,' and 'clinical.' Second, various indices of practical and clinical significance are briefly reviewed. Finally, it is argued that counselors should not consider only statistical significance when conducting inquiries or evaluating research reports.
>
> Practical or clinical significance, or both, will usually be relevant in most counseling research projects and should be explicitly and directly addressed. Authors should always report one or more of the indices of 'practical' or 'clinical' significance, or both. Readers should expect them. And it is argued in this article that editors should require them."

Substantiating his arguments that statistical rigor was important, Thompson quoted Boring as follows,

> "For example, in his critique of the mindless use of statistical tests titled 'Mathematical vs. Scientific Significance,' Boring (1919) argued some 80 years ago, 'The case is one of many where statistical ability, divorced from a scientific intimacy with the fundamental observations, leads nowhere' (p. 338)."

The field of education and psychological testing have adopted the term "effect-size" as an important tool accounting for the sample size in a given experiment compared to a similar experiment in a larger pool of subjects. Thompson noted,

> "Given considerations such as these, Roger Kirk titled his Southwestern Psychological Association presidential address "Practical Significance: A Concept Whose Time Has Come." Kirk (1996) emphasized that statistical significance tests only evaluate "ordinal relationships" (e.g., whether two group standard deviations are different or one is larger than the other). He argued,
>
> > Is this any way to develop psychological theory? I think not. How far would physics have progressed if their researchers had focused on discovering [only] ordinal relationships [such as those tested by conventional null hypothesis tests]? What we want to know is the size of the difference between *A* and *B* and the error associated with our estimate; knowing *A* is greater than *B* is not enough. (p. 754)
>
> This emphasis on quantifying findings in service of evaluating the practical noteworthiness of results also is not new. For example, long ago Fisher (1925) advocated the calculation in ANOVA of the index called eta squared (or the correlation ratio). Similarly, Kelley (1935) proposed another ANOVA index of practical significance: epsilon squared. These indices have generically come to be called "effect-sizes." There are literally dozens of available choices. Various syntheses of these choices are available (cf. Kirk, 1996; Olejnik & Algina, 2000; Snyder & Lawson, 1993).
>
> Effect-sizes are particularly important because statistical tests are so heavily influenced by sample sizes."

Summarizing his goal, Thompson noted,

> "**Why Effect-size Interpretation Should Be Required**
>
> As readers know, the 1994 American Psychological Association (APA) Publication Manual incorporated an important revision "encouraging" (p. 18) authors to report effect-sizes. However, there are now 11 empirical studies of either 1 or 2 volumes of 23 different journals demonstrating that this encouragement has been ineffective (Vacha-Haase, Nilsson, Reetz, Lance, & Thompson, 2000)."

It does not appear the situation has changed since 2002 with regard to the field of vision, although a large majority of the journals in the field of education and psychology have adopted policies "requiring" that effect-sizes be reported. Thompson provided a variety of calculations showing the conversions between various closeness of fit calculations.

Skidmore[131] & Thompson reported that,

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[131]Skidmore, S. & Thompson, B. (2011) Choosing the Best Correction Formula for the Pearson r^2 Effect Size *JExper Educ* vol 79(3), pp 257-278

> "By 2006, more than 24 journals, including the flagship journals of the American Counseling Association and the Council for Exceptional Children (both with more than 50,000 members) promulgated explicit effect-size reporting expectations in their author guidelines. For example, the author guidelines for The Journal of Experimental Education say to "interpret magnitude-of-effect measures in conjunction with every p value that is reported."
>
> "However, one of the problems with effect-size interpretation may be that authors do not recognize the effect-sizes produced in their own analyses. An analysis of statistical techniques in the American Educational Research Journal and the Journal of Counseling Psychology reported that 'some authors routinely report bivariate and multiple correlation coefficients, without recognizing these as effect-size indices and without interpreting them in relation to related previous effect-size reports' (Kieffer, Reese, & Thompson, 2001, p. 304). This is disconcerting especially because the Publication Manual specifically includes the Pearson r and multiple correlation coefficient (*R*) as examples of effect-sizes, and numerous scholars have written about effect-sizes (Grissom & Kim, 2005; Kirk, 1996; Thompson, 2006b, 2007)."

Skidmore & Thompson also provided a comprehensive review of various effect-size related errors in both r^2 and R^2 formulations. There results stress the importance of using a cohort of at least 40 to avoid most errors associated with Pearson's r^2 values. ***Errors for a cohort smaller than 20 can be dramatic!***

1.3.5 Needs for careful experimental design and implementation

At the detailed level, many problems associated with experiment implementation are similar to the problems of experiment design. These generally concern the precise control of the various parameters affecting the results once they are recognized as important.

A vast majority of the papers in the vision literature suffer from poor or inadequate experimental design. If there is a primary shortcoming, it is the lack of sufficient data collection to define an adequate mathematical confidence level in the results. It is interesting that in an era when television news programs have found it necessary to indicate the confidence level in their surveys, the same has not occurred widely in the vision research arena. It is rare that only two to 10 subjects can provide statistically relevant data concerning the performance of a complex system such as vision.

For the new investigator, the remarks of Barford[132] comparing the work of Jenkins and Robinson should be reviewed. Many texts are available today on the design of experiments. Unfortunately, many of them limit themselves to linear systems in order to use matrix algebra and numerical analysis via digital computer using simple algorithms. The visual system is grossly nonlinear, involves many state variables and is not generally amenable to first order matrix calculations. Nevertheless, the first Chapter of Weber & Skillings[133], or similar material, should be reviewed before beginning any laboratory investigation.

1.3.5.1 Problems found most frequently in psychophysics

1.3.5.1.1 Use of "stock instrumentation"

Experimental techniques in psychophysics have probably relied too long on the use of packaged test equipment instead of the precise quantification of the variables affecting their results. Most test instrumentation of the current era provides many test modes and features. The mode used and the particular capabilities of that mode must be defined. The classic case is using a light source and only defining the voltage (or the current) at which it is operated. This is not an adequate description of the spectral content of the radiation emanating from the "glass" enclosure of the source. Photometers are another source of considerable error if their spectral absorption characteristic and their method of detection, quantum using a photoelectric detector or energy using a thermal detector, are not specified.

1.3.5.1.2 Use of difference spectra

Using difference spectra imprecisely in psychophysics has been common. They have frequently been used because of their experimental simplicity. Difference spectra are usually defined in one of two ways. The simplest involves linearly subtracting a measured spectrum under conditions of chromatic adaptation from the non-real C.I.E

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[132]Barford, N. (1967) Experimental measurements: precision, error and truth. Reading, MA: Addison-Wesley, preface and pp. 1-24, 41-44, & 72-80 as a minimum

[133]Weber, D. & Skollings, J. (2000) A first course in the design of experiments. Boca Raton, FL: CRC Press

luminosity functions of the Standard Observer. Besides the fact the C.I.E. spectrum is totally synthetic, it has also been smoothed and does not exhibit the actual features of the real luminosity functions. Therefore, results using this technique can be an approximation at best. The alternate method involves comparing the luminosity function under two different states of adaptation. In this method, it is common to consider the natural or unadapted state as described by the spectral response of one putative broadband chromophore. The linear difference between this spectrum and the second obtained under conditions of spectral adaptation is then an indication of the spectral response of a second putative chromophore.

Both of the above methods suffer from two distinct problems. The actual visual system does not generate the perceived psychophysical response based on a linear summation. Therefore, taking a linear difference is essentially meaningless. The results do not accurately portray the operation of the system, or its constituent chromophores. Second, using chromatic adaptation to suppress one putative chromatic channel by a factor of about 100:1 is common. However, this level of adaptation is inadequate. As will be shown in detail in **Chapters 16** & **17**, this degree of suppression only results in an enhanced Brezold-Brucke or Purkinje Peak, the former near 487 nm and the later near 580 nm. To determine the spectrum of the long wavelength chromophore, the mid wavelength chromophore must be suppressed by at least 1000:1 to obtain an accurate representation. When this is done, the actual peak of the long wavelength chromophore, near 625 nm is obtained. When inadequate suppression is employed to measure the long wavelength peak and the data is smoothed, either by using wide spectral filters or by using inadequate filter spacing, a peak response can be obtained at any wavelength between 532 nm and 625 nm. The prominent Purkinje Peak at 580 nm frequently dominates the approximation. It is the peak in the region of 575-580 due to the Purkinje Effect that is usually reported as the peak of the long wavelength chromophore in psychophysical experiments. Both the Brezold-Brucke and Purkinje peaks are perceived artifacts due to the logarithmic signal processing in human vision.

1.3.5.1.3 Use of inadequately documented tri-color cathode ray monitors

Although able to reproduce "color" information much more faithfully than current electroluminescent and liquid crystalline types of tri-color displays, the spectral capabilities of tri-color cathode ray monitors should be carefully documented. As an example, the phosphors used in "standard" European tri-color monitors for television are different from those used in "standard" North American tri-color monitors. So, their spectral performance is different. The phosphors used in computer and industrial monitors introduce another degree of freedom that must be quantified.

For those experimenters relying on the conventional wisdom that the long wavelength chromophore of vision peaks near 576 nm, it is instructive to note that most tri-color cathode ray monitors emit virtually no radiation in this spectral region[134]. The integral of the product of the emission spectrum of the typical monitor and the putative 576 nm spectrum of the eye as a function of wavelength is near zero relative to the similar calculations for the short and medium wavelength visual channels. Recognizing that the spectral response of the long wavelength chromophore actually peaks at 625 nm resolves this difficulty.

1.3.5.1.4 Problems with the use of the Bayesian Approach

The 19th Century English mathematician Thomas Bayes formalized the concept of inverse probability–this being the technical term for the likely cause of an effect, rather than the probable effect of a cause.

Hodges provided an analysis of this technique[135]. "The basic idea was nothing but the common sense calculation of "likeliness" of a cause, such as people would use all the time without thinking." He pointed out two critically important facts. First, "It was very important to bear in mind that experiments could only produce relative changes in 'likeliness,' and never an absolute value." Second, "The conclusion drawn would always depend upon the a priori 'likelihoods' which the experimenter had had in mind at the beginning."

The critical point is that the experimenter must identify all of the potential causes of an event before performing the experiment and allocating likelihoods to those causes. If there is a cause that was not identified, the results will not reflect that cause. In this case, the likelihoods assigned to other causes will be excessively high and inappropriately distributed (and frequently misleading).

Stone has provided a thorough review of the use of the Bayesian Theorem as of 2012[136]. His formulation stresses the "prior" environment with respect to the correct perception of an image focused on the retinal. When discussing the

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[134]Hunt, R. (1991) Measuring color, 2nd ed. NY: Ellis Horwood, pg. 128
[135]Hodges, A. 1983) Alan Turing: the Enigma NY: Simon & Schuster, pg 196
[136]Stone, J. (2012) Vision and Brain: How we perceive the world. Cambridge, MA: MIT Press pp 156-178

perception of a new image, he notes the perceived image depends on the image data provided and the learning experience associated with a similar image earlier. Such a prior encounter results in a "prior expectation" related to that earlier image.

perceived image = image data + prior expectations

More formally, he expresses the relevance of the prior in calculating the posterior probabilities as used in the theory of inverse probability;

posterior = k x likelihood x prior

Lacking an adequate model, many psychophysical experimenters have attempted to use the Bayesian approach inappropriately and published less than accurate results.

The problem of "prior" is similar to the problem of estimating the number of degrees of freedom when using multi-dimensional scaling. As an example as developed in this work, there are four chromatic photoreceptors in the retina of human vision. If one assumes there are only three, one never identifies the ultraviolet channel receptor and the measured performance of the visual system remains incorrect (or ambiguous) in the region between 400 nm and 437 nm. This difficulty has been encountered multiple times beginning in the 1930's. In the case of MDS, setting the number of nodes related to the data at three chromophoric channels will negate chances of identifying the fourth channel.

Stone's conclusions on pages 174-178 are worthy of serious study. **Section 4.6.3** of "The Neuron and Neural System" addresses the transition from recognition based on priors to detailed analyses associated with the presentation of non-prior imagery. This latter learning function (training) is of major importance in neural systems.

1.3.5.2 Problems found in electrophysiology

1.3.5.2.1 Incongruity between *in-vitro* experiments and *in-vivo* operation

The expression *in-vivo* and in-vitro frequently appear in the titles and introductions to papers in the literature. As time has gone by this binary distinction has become less and less adequate. It is becoming ever more difficult to define *in-vitro*. Often complete cells are kept "alive" with metabolic feeding and other techniques. However, they are frequently deprived of the required electrostenolytic nutrients. One must strive to be more precise in defining current test situations and in making comparisons with the literature.

A major problem in interpreting the literature arises from the changes in conditions related to *in-vitro* tests and the conditions present during *in-vivo* operations. A particularly significant case involves the many voltage clamp experiments performed and reported over the years. The in-vitro experiments have invariably removed the source of the potential the experimenters were attempting to quantify and define. They have also routinely washed the neurons and thereby removed the intrinsic source of potential powering the Activa of the neuron. As a result, most of the experimenters have carefully evaluated their test set using a protocol that was insufficient or that they did not properly interpret. On the other hand, the in-vivo experiments involved an uncontrolled variable associated with the conexus that the protocol did not recognize.

1.3.5.2.2 Use of dim light

An unusual expression appears repeatedly in the experimental literature of vision. The expression is that the experiments were carried out under a "dim red light." This appears strange to a photographer. If the "dim red light" is bright enough to affect the experimenter's photoreceptors after bouncing diffusely off the material being examined and then passing through the very small aperture of the experimenter's eye, why is it not bright enough to affect the material itself? The incident radiation at the material is at least 100 times brighter than on the experimenter's retina. In working with film in a dark room, no light is allowed at all until after the initial development process has occurred and the transduction process has been completed. At this point, the dyes used to sensitize the emulsion have been removed or deactivated. Using a "dim red light" is then permissible because the silver halides themselves, while still sensitive to blue and green light, show negligible sensitivity to red light. Photographic printing papers are specifically designed not to be sensitive to dim red light as exemplified by the trade name, Safelight. A Safelight cannot be used in a dark room where panchromatic or "color" film is being processed until after the emulsion has been desensitized to red light. In vision, this means that **a Safelight cannot be used at all** if the long wavelength chromophore is of technical interest. Some recent work has used infrared light and infrared goggles to avoid the uncontrolled "bleaching" of the long wavelength chromophore.

If the experimenter is to obtain valid results related to the sensitivity of the various chromophoric materials of

vision, it is important that all visible light is eliminated during the experiments. Alternately, the light can be treated as a controlled and measured variable. "Bleaching" is frequently a cumulative process when the chromophoric material is dissociated from the neural connections of the Inner Segment (IS). Performing experiments under dim light just means, the cumulative effect of the light takes longer to reach a significant level. Thus, if the material is exposed to 5, 50 or 500 seconds of "dim light" can be a quite significant fact. Experimenters should take pains to control this parameter.

An interesting data set is available in the literature related to the determination of the spectral response of the human subject under various conditions. It is interesting in that it appears that the subject was allowed to smoke a cigarette during a break, or at least he looked briefly at something red--possibly a red exit sign. The result was a significant discontinuity in the data set concerning the L-channel of vision that cannot be explained based on the planned and described experiment.

The importance of controlling the illumination level when working with chromophores, either *in-vivo* or *in-vitro*, will be explored further in **Section 6.6.**

1.3.5.2.3 Temperature Control

Reporting the temperature of the specimens during examination to a precision of a few degrees Celsius and an accuracy that is completely unknown is common in the literature. The temperature is usually measured at some remote point relative to the specimen. To achieve the accuracy necessary to contribute meaningful data to the current literature, it is important that the temperature of the specimen be known and recorded with an accuracy of at least 0.5 degrees Celsius. Otherwise, the data can only be compared with similar data by plotting with a very broad brush. If the temperature of the subject is inferred relative to some nearby substrate, the method of inference should be documented. This proposition will be developed further in **Appendix A**.

1.3.5.2.4 Appropriate electrical grounds

Using the proper signal return path is extremely important during experiments. The animal eye employs three local ground connections interconnected by relatively poor electrical conduits. The first local ground is within the IPM and supports the Outer Segment and the outer portion of the Inner Segment of the photoreceptor cells. This local ground is separated from the second local ground found within the INM that supports the remainder of the photoreceptor cells, all of the signal processing within the retina and the action potential generation portion of the ganglion cells. The third local ground is associated with the brain. This local ground is connected to the local ground in the INM by a relatively high impedance path parallel to the optic nerve. The existence of three separate local grounds leads to significant ground loop currents if the appropriate ground connections are not contacted by the signal return lead.

The presence of separate local grounds is most easily demonstrated by the recording of an ERG. In recording the ERG, the signal lead normally contacts the outer surface of the eyeball. This is a location that would not exhibit any electrical activity except for the poor conductivity between the IPM and the INM. This poor conductivity is due to the presence of the Outer Limiting Membrane. The OLM causes all of the return path current between the INM and the IPM to pass along the outer surface of the eyeball. By connecting the return lead of the test set to an even more remote portion of the animal's anatomy, a voltage signal is measured that represents the voltage at a point along the ground path between the IPM and the INM, and an undefined electrical surface. This return lead is usually labeled either the reference electrode or the indifferent electrode. The DC component of the signal measured in this way has little meaning. However, the AC component has been used to study the performance of the photoreceptors under various conditions of stimulation.

The recorded signal is roughly proportional to the number of photoreceptors excited. This is exactly what would be expected if the total return current from all of the excited photoreceptor cells was passing along the surface of the eyeball.

1.3.5.2.5 Inadequate bandwidth and sampling in spectral measurements

Although it is old data, the data of Von Studnitz from 1932 illustrates clearly the problem of using inadequate spectral measurement instrumentation[137]. The data shown is quite distorted compared with the dotted curves provided by Crone, which are in themselves questionable with respect to precision. The caption for the figure says "Absorption curve of snake cone pigments, with three maxima" with the word curve in the singular. A single curve would be more appropriately labeled the luminous efficiency function of the snake. The efficiency function when

[137]Crone, R. (1999) A history of color. Boston, MA: Kluwer Academic Pulbishers, pg. 218

measured with a spectral bandwidth of less than 10 nm would show additional structure related to the logarithmic summation in the visual system and the resulting Brezold-Brucke phenomena.

1.3.5.3 Problems found in relating physiology and genetic

It is an early day in genetic research, although it is moving forward with the speed expected at the start of the 21st Century. However, a close relationship between physiology and genetics is still not well established at the detail level, primarily because of a lack of an adequate model defining the mechanisms and processes of the visual system. An example is the search by the geneticists for a triplet of code positions that would relate to the three chromophores postulated by the trichromatic theory. It would be more realistic to search for a quartet of code positions suggested by the more general case of the tetrachromatic theory. A second example involves associating certain genetic problems with achromatopsia without a complete understanding of the electrophysiology of achromatopsia. This situation will be discussed in detail in **Chapter 18.**

The same problems as in **Section 1.3.5.1.2** have been found in more fundamental approaches to chromophore determination. In 1991, Oprian, et. al[138]. claimed to have been first to obtain spectra from isolated human color vision pigments that they grew from "cone" cells with modified genes. They obtained correct estimates of the spectral peaks at 424 and 530 nm in *in-vitro* experiments but obtained a value of only 560 nm for the long wavelength chromophore. This value leaves open the question of the precise nature of the actual chemical material used to obtain their final spectral recordings. Whether their material was in the liquid crystalline state during their experiments, could not be determined from the text. It is also not clear why they were unable to grow the individual pigments in separate culture dishes to avoid the need for difference spectrum experiments.

1.3.6 On-going dispute between the psychology and the lighting & display schools

There has been a long standing argument (more than a debate) between the psychology community and the engineering community over the spectral performance of the human eye dating from the 1930's and most intense during the 1970's through the 1990's. Romney touched on this difference in 2009[139]. Because of a difference in protocols (both relying on the linearity assumption of Grassman), the psychology community promulgated a tricolor spectral sensitivity for the human eye with the peak sensitivity of the long wavelength channel in the yellow region (peak wavelength ~564 nm). This peak value is inconsistent with much of the psychophysical data acquired by the psychology community itself and is in gross conflict with the engineering community and the inability of industry to build an television or printing system based on a long wavelength photoreceptor with a peak at less than 600 nm. This conflict will be addressed cytologically in Chapter 4, **Sections 4.6**, resolved chemically in Chapter 5 (**Section 5.5**, specifically **Section 5.5.10**) and demonstrated operationally in Chapter 17 (**Section 17.3**).

While the psychology community has maintained control of the academic press in this area, make no mistake; The spectral performance of the human and mammalian eyes exhibit first order peaks at 435, 532 and 625 nm as confirmed in practice and throughout industry. Second order chemical theory might support the long wavelength photoreceptor peaking at 600-605 nm but not at any shorter wavelength. Laboratory experiments have not shown adequate precision to resolve this potential shortening.

1.3.7 Experiment Reporting

Page limitations in the various periodicals play a deleterious role in vision research. They force reports to assume the form of a Reader's Digest article rather than a comprehensive document. The experimental configuration is seldom reported with any degree of adequacy in the literature. This makes it difficult to determine the actual parameters used when the investigator, who may be unaware of it, has failed to specify certain parameters. A common example is the specification of a light source by its input wattage, as opposed to its spectral characteristics (at least its color temperature) and its illuminance (or the luminance at the subject). The coming of the INTERNET has largely alleviated this problem. Future authors should be expected to provide a comprehensive document to a website with only a condensed version published in a journal.

1.4 Perspective

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[138]Oprian, D. Asenjo, A. Lee, N. & Pelletier, S. (1991) Design, chemical synthesis and expression of genes for the three human color vision pigments. *Biochem.* vol. 30, pp 11367-11371

[139]Romney, A. & Chiao, C-C. (2009) Functional computational model for optimal color coding *PNAS* vol 106(25), pp 10376-10381

This Work was undertaken after many years of conceptual development in the field and the successful application of many pieces of the overall theory in the aerospace field. It was intended that this work collect these conceptual pieces and integrate them, with other literature, into a unified theory and global model of the mammalian visual system (with direct extensions to other classes in the phylum). The resulting theory would be;

internally consistent,
consistent with the experimental literature and
mathematically precise.

Although the purpose is not to take exception to many precepts of the psychophysical community, such action is necessary. The position taken by the Committee on Colorimetry of the Optical Society of America as late as 1963 could use some further examination when it says:

> "The use of quantitative concepts would specialize the relational definitions (used in the psychophysics of color) in an undesirable manner." (The Science of Color)

As a result, this community uses an inaccurate description absorption spectrum of the long wavelength chromophore to this day.

This archaic position is stressed to compare it with the recent and opposite position taken by the National Science Foundation in Chap. 10 of their 1996 Program:

> "Characterization of biological systems has reached an unparalleled level of detail. To organize this detail and arrive at a better fundamental understanding of life processes, it is imperative that powerful conceptual tools from mathematics and the physical sciences be applied to frontier problems in biology."

The National Science Foundation goes on to say:

> "Modeling of biological systems is an important partner of experimental work. All facets of biology--environmental, organismic, cellular, and molecular--are accessible to chemical, physical, and mathematical approaches. The Foundation encourages increased collaboration among physical scientists, mathematicians, and biologists in addressing biological problems. "

It has also become a goal of this work to provide citations to some older but valuable experimental work that is crucial to an accurate understanding of the eye, particularly in humans. This data is becoming difficult to find because of its age. The policy of most libraries to move older material to more physically and functionally remote archives aggravates this problem.

This work will incorporate much information and many techniques that have not been available to the typical vision investigator; they have been developed in domains outside the purview of "the club." This situation will most surely aggravate many in "the club." In a sense, this author must call on the well-known defense; feel free to attack the message but please do not attack the messenger.

In preparing this work, it has often been found that recent authors have omitted the caveats of earlier workers when they quote their work. This has led to the presentation of many unfounded conclusions. Going back to primary sources has frequently been necessary to avoid this problem of building on incorrect propositions. Going back to original sources, leaves this work open to the criticism of "relying on old data." However, returning to old primary data is better than to continue to propagate errors introduced by more recent authors.

Phylogeny– It became useful early in the program to explore the characteristics of the eyes in animals of other Phyla than *Chordata*. The intent was to show the important features and limitations through comparison among the different animal eyes. It soon became apparent that the widely used bipartite phylogenic tree of the animals (separating the protostomic from the deutrostomic) was not consistent with the evolution of eyes. The evolution of vision was represented better by a tripartite phylogenic tree focusing on the three Phyla, Arthropoda, Mollusca and Chordata. In this construction, the phylum, Annelida, was considered a continuation of the precursor to the above three Phyla. With respect to vision, it has not evolved very far from the earliest times.

Optics– Many recent investigators have explored the optics of the eye without a clear understanding of the many caveats that apply. They frequently invoke "Standard Eyes" derived by Gullstrand or LeGrand without recognizing the assumptions contained within these models. They seldom note the fact that Gullstrand derived so many different "Standard Eyes" that he numbered them. From the perspective of an optician, four digits after the decimal point is absolutely minimal in modern calculations. However, many authors have truncated the values of the original authors

to as few as two places. Wyszecki & Stiles[140] present the most complete sets of parameters for the optics of the human eye but they do not present all of the relevant caveats. To appreciate the caveats, the updated translation of LeGrand by LeGrand and El Hage is recommended[141]. It should be recognized that many values in their book have been rounded to 2 decimal places for pedagogical purposes. They stress that the paraxial, i.e., Gaussian, approximation cannot be applied to the general eye (page 58). They go on to say the paraxial approximation is adequate for and normally used in optometry. A variety of caveats are addressed on pages 4, 7, 58, & 61-63. **Appendix L** will review the pertinent optical theory.

Neuroscience– The state of the art in neuron research is epitomized by the statement by Marshall & Zohar in **Section 1.1**[142]. This work will introduce a completely new interpretation of the neural system in animals that takes advantage of the immense experimental data base available. However, it necessarily introduces new terminology drawn from the physical sciences and engineering. The resultant theory and description of the neuron explain most of the outstanding questions concerning the operation of the neural system.

General guides– To aid both the people new to the field of vision research and the experienced participant, providing some guideposts before proceeding to the details of this work is useful. This work rests on the fundamental propositions that the visual system in animals;

+ is based on well known electronic phenomena,

+ is consistent with the rules of chromophore (dye) chemistry,

+ uses Vitamin A only as a chromogen, or precursor to the true chromophores of vision,

+ uses the constituents commonly related to the sources and uses of energy in the animal, such as ATP, ADP, GTP, various G-proteins and kinases, to perform the same function in vision but does not involve them in the signaling function of neurons This is particularly true of the glutamates. They are primarily associated with the cell wall and used to release energy by acting as the analogs of electrolytes in a battery.

+ uses a neural signaling system based on a series of electrolytic conduits and active electrolytic semiconductor devices, Activa. These devices are analogous to but different physically from man-made transistors.

+ uses a very sophisticated portion of the glutamate cycle of nutrition that is chemically reversible and therefore highly conservative in the use of energy.

The resultant theory is much simpler and more comprehensive than competing theories. **It also allows the description of a single end-to-end model of the visual function.** However, accepting it initially may be difficult for some readers with preconceived ideas.

1.4.1 The role of an Epicurean

A significant problem exists to this day in the attempts by biologists and psychophysicists to ignore and even deprecate the work of theoreticians and investigators from “outside their field.”

> Quoting Park on the natural human condition[143]: "Outside a small circle, people greet the philosophy of Epicurus [any outsider] with the special rage and scorn reserved for those who question prevailing beliefs."

To illustrate how small the circles are in the field of vision and neural research, there are major philosophical and theoretical differences between the editorial boards of the professional journals. Lacking detailed models, their technical positions have diverged to the point where they actually conflict. An author must be sure to select a journal compatible with his reading of the conventional wisdom if he expects to be accepted for publication.

This has led to the stalling of the overall field alluded to above. It has also led to a group of conceptual models that attempt to avoid making intrusions (waves) into the domain of the other camp. Thus, the literature contains an

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[140]Wyszecki, G. & Stiles, W. (1982) Color Science. NY: John Wiley & Sons
[141]LeGrand, Y. & El Hage, S. (1980) Physiological Optics. NY: Springer-Verlag.
[142]Marshall, I. & Zohar, D. (1997) Who’s afraid of Schrodinger’s cat? NY: William Morrow pp. 23-24
[143]Park, D. (1997) The fire within the eye. Princeton, NJ: Princeton University Press. pg. 10

arbitrary division of photoreceptors into luminance types (rods) and chrominance types (cones) except when the experimentally collected data produced chrominance sensitive rods ("red-rods', 'blue' rods and 'green' rods). It is interesting that data supporting reports of rods (or cones) sensitive only to broadband luminance are rare or nonexistent. Similar shorthand notation developed by various schools is frequently misinterpreted by later investigators. The Hering school of the 1950-1960's frequently referred to a black-white sensitive opponent "channel" which implied a black sensitive photo receptor, in analogy to the photoreceptors in the other proposed opponent channels. Later, this led to descriptors like "OFF surrounds" which actually related to a reduction in a net stimulus and not its removal. Adopting a more global, mathematically oriented, model quickly clarifies and rationalizes these concepts.

If separate classes of rods and cones are accepted, there must be a region of overlapping performance between them. The concept of rod intrusion into cone operations frequently appears in textual material but a more precise description of the effect is virtually absent from the literature. Schanda gives a short hand formula for determining when rod intrusion is significant but he does not present any theoretical or mathematical description of the effect[144].

1.4.2 Modeling Philosophy

The subject of models has frequently been quite controversial in the Visual community. Not wishing to enter this argument, several quotations from Harmon & Lewis[145] will be used to accompany this overt model; "The making of models *is universal* in the search for a consistent and instructive picture of nature." " By *overt modeling*, we mean studies explicitly designed to complement experimental neurophysiology, not the tacit modeling that always accompanies experimental design, measurement, description, and interpretation of results."

"An important part of the utility of a model lies in its ability to focus disparate evidence and interpretations into one coherent view; parsimony of explanation often leads to revealing unity. Models are also valuable to the extent that they raise new questions and suggest new relationships, perhaps leading to new experiments that might not otherwise have been considered. Worthwhile models are predictive; that is, new relevant properties are deducible from them. Further, a model often suggests constraints that may exist in the system being modeled. If these constraints are valid, they can serve to guide subsequent experimental interpretation. Thus to reveal, test, compute, extrapolate, and predict is to accelerate the process of learning about the real world."

"Models are a necessary ingredient of scientific method: as deductively manipulatable constructs, they are essential to the evolution of theory from observation."

1.4.2.1 The Goal of this work

The above quotations speak eloquently of the goal of this work and hopefully the methodology used. **The goal of this work is to provide a detailed comprehensive model of the visual system that is completely supported by rational block diagrams and the mathematical framework behind it.** The model must be compatible with the visual systems described in the phylogenic tree of **Section 1.2**. It must alsoprovide answers to thought experiments that are mathematically defendable and compatible with the subsequent laboratory investigation. Finally, it must be sufficiently precise mathematically to support statistical analyses of measured data and allow further expansion based on subsequent experiments in vision.

1.4.3 Tests of a good Model and/or Theory

Few attempts to describe the quality of a good model or theory are available in the vision literature. One set of criteria, found in Harmon & Lewis, is:

+ First, and mandatory, preliminary validation by testing the model's accuracy by matching the model's behavior with physiological observations.

+ Second, attempt to discover new properties of the model (i. e. operations not explicitly considered in the original design). Then determine if these properties are found also to be characteristic of the biological system.

+ Third, test new hypotheses drawn from the work of laboratory investigators against the model

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[144]Schanda, J. (1998) Current CIE work to achieve physiologically-correct color metrics *In* Backhaus, W. Kliegl, R. & Werner, J. *eds*. Color Vision" Perspectives from different disciplines. NY: Gruyter pg 314

[145]Harmon, L. & Lewis, E. (1966) Neural modeling. Physiological Revue 46: 513-591

> and see if correct results are obtained faster and earlier than can be obtained through experimentation.

If the model can succeed in the above three tests, it can be considered a valuable asset and additional effort is justified in progressively expanding the model as the field of knowledge expands.

1.4.4 Modeling Scope

Harmon & Lewis also discuss two distinct modeling philosophies, focusing on the selection of parameters in neural modeling. Each has important applications. In the first, a very large number of neural properties are reproduced with high accuracy. Here, the complete model may become unwieldy and simplifying it for a specific application is frequently advisable.

In the second case, a more restricted set of properties is used to create the model. It is then assumed that such a "minimum parameter" model has retained the important parameters. It is also assumed that incorporating more parameters is possible as it becomes necessary to do so.

It is very unfortunate but true that the second approach has been used too often in vision research and subsequent extensions of the simple model have been ad-hoc. These ad-hoc extensions have usually been adopted without a comprehensive review of the galaxy of possible extensions. That has led to many inappropriate research paths and misleading results.

1.4.5 Models prevalent in the neurology literature

This subject will be addressed in more detail in **Chapter 10.** However, it needs to be addressed here for continuity. Hille in 1992 addressed the subject of "What are models for?" His thoughts are instructive[146]. He had just concluded several chapters that sought to understand axon excitability using several physical and kinetic models and said:

> "We have seen the Hodgkin-Huxley model with its voltage-dependent *h*, *m*, and *n* gating particles and with open channels obeying the Nernst equation and Ohm's Law. We have seen the constant-field theory of Goldman, Hodgkin, and Katz with ions moving independently through a continuum, barrier models with ions hopping among a small number of saturable sites, Gouy-Chapman-Stern models of surface potentials, Woodhull blocking models, and state-dependent schemes of toxin binding. None is a true molecular theory derived from first principles. Each is an idealization with such simple assumptions that we can hardly expect any real case to obey them [sic].
>
> What is the scientific value in making models that are so easily criticized? The answer lies in several directions. First, the model is proposed to explain specific observations . . . Second, modeling stimulates and directs measurements."

Hille did not address the danger of adopting inappropriate models that can lead the researcher astray. None of the models used by the above investigators employed an adequate model of a viable biological membrane. This is due to two primary factors. They were all unaware of the liquid crystalline state of matter and its crucial role in the characteristics of the biological membrane. Second, they were all unaware of the field of semiconductor physics that described the electrical performance of the liquid crystalline biological membrane. Without this awareness, they were unaware of two critical facts. The fact that free electrons can pass through biological membranes (independent of any atomic particle) and the fact demonstrated in this work that these free electrons are the dominant form of charge transport across neural membranes. Hodgkin & Huxley stated that their ionic currents flowed in the correct direction and were of the correct order of magnitude. This is correct, but their ionic currents were approximately 5:1 smaller than the dominant electron currents. Yudilevich expressed the narrow perspective of the common wisdom in the Preface of a text in 1991[147] with the statement: "The field of transport of solutes across cell membranes is of wide interest and at the cross roads of basic and applied Medical Sciences. The discipline covers a wide range of science from Physiology to Molecular Biology." Why was the transport of electrons across cell membranes excluded? Whereas the transport of solute across a membrane is critical to the metabolism of any cell, it is the transport of electrons that is critical to the signaling function of the neuron.

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[146]Hille, B. (1992) Ionic channels of excitable membranes. 2nd Ed. Sunderland, MA: Sinauer Associates. pp. 502-503

[147]Yudilevich, D. Deves, R. Peran, S. & Cabantchik, Z. (1991) Cell membrane transport. NY: Plenum Press pg. v.

Hille also stated: "Hodgkin and Huxley (1952d) gave a two-parameter formula adequate to describe the macroscopic features necessary for regenerative excitation of action potentials. Their model is formally equivalent to a highly symmetrical, eight-state diagram. We now believe that gating involves transitions among at least eight states, but the rate constants do not show the strict symmetry that allowed HH to summarize a seventh-order system in terms of two first-order processes (transitions of *m* and *h*). Instead, we are left with descriptions that can be explored only by computer calculations." The computer calculations referred to are not closed form solutions of definite integrals but numerical iterations performed against assumed initial conditions until a result is obtained that appears reasonable. Since any number of reasonable results can be obtained in this manner, the results have little theoretical weight. This work does not support the gating belief.

None of the electrical circuit models prevalent in the electrophysiology literature of neurons is relevant to the actual operation of the neuron. To be substantive, a model must not only express reasonable results, it must be based on the relevant fundamental physical sciences. Here, the relevant physical sciences include the semiconductor physics of the liquid crystalline state of matter.

1.4.5.1 Floating Models

Wyszecki & Stiles[148] spend several pages discussing the philosophy of theories and models with limited results. Overall, they fail to define a theory, only discussing some of its characteristics. For the purposes of this work, a theory is a comprehensive statement of the postulated manner in which a visual system works based on the empirical evidence taken as a whole. A theory is usually interpreted more completely through a series of postulates and the use of a model, frequently graphical, describing the more detailed concepts stated in the theory. It is extremely important that the model, or individual detailed sub-models, remain consistent with the postulates of the overall theory.

They do discuss the idea of a "floating model" at some length. They say it is encountered quite frequently in vision research. This is an understatement. Essentially a floating model is based on a narrow series of empirical facts but it is not shown to be mathematically compatible with an overall theory or higher level model. Such ***a floating model should not be relied upon*** since it involves a series of assumptions that:

+ may or may not be stated adequately and explicitly

+ cannot or have not been shown to relate to any overall theory.

The principal purpose of this work is to present an overall theory, and a series of submodels, that are internally self-consistent and in total agreement with the ***overall empirical data base***. A single model is not presented only because it is so extensive that it cannot be properly appreciated as a whole. The partial model, labeled the Top Level Schematic of the Chordate Visual System, to be presented in **Figure 1.5.2-2** strains the capability of most people to comprehend a complex network. Therefore, simpler models will appear throughout this work. However, be assured that all these models are consistent with the overall theory and the top level model.

This work may not be consistent with the many floating models in the literature that do not enjoy any traceability to a more comprehensive model. These floating models have been defined to explain a small area of data in the overall empirical data base. It will, where possible, show the questionable assumptions upon which the various floating models are based.

1.4.6 Necessity of employing nonlinear techniques

DeVoe, writing in Bernhard, probably said it best: "It is, in general, a dubious proposition to study the properties of a nonlinear system in terms of its small-signal, linear behavior, inasmuch as the linear behavior is more apt to be a special case of the nonlinear behavior than vice-versa[149]." This is manifestly true in vision where a fundamental logarithmic transformation and a highly nonlinear adaptation process are the key element in the signaling architecture of the visual system. Figure 4 in DeVoe clearly shows the asymmetry of the visual response under large signal conditions.

Reliance on the linear "color equation" of vision for the last three-quarters of a century has been a major impediment to understanding the visual process.

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[148]Wyszecki, G. & Stiles, W. (1982) Color Science. 2nd Ed. NY: John Wiley & Sons pg.582-587

[149]Bernhard, C. (1965) The Functional Organization of the Compound Eye. NY: Pergamon Press. pg. 311

1.4.7 The fundamental concepts of the visual and neural systems

This work has surfaced a long list of new principals upon which the visual and neural systems of biology are founded. Many of these conflict with the conventional wisdom. This section will highlight only the major principals that will require a paradigm shift in the thinking of many people previously active in the field. The other changes are summarized in **Section 1.5.3.2** and will be introduced as appropriate within the main text. Complete references are provided in the cited Sections and Chapter of this work.

The shifts developed below are solidly founded on the data of the literature. Their implementation has led to the definition of a comprehensive, multidimensional, model of the complete visual-neural system of biology. This global model supports multiple descriptions of the visual and neural processes. It also supports a rigorous mathematical description of these processes. The fully elaborated mathematical description becomes unwieldy. However, it can be simplified. Equations describing the output of the visual/neural system as a function of any individual input (or few inputs) can be obtained by setting the other variables and internal parameters to appropriate *in-vivo* values.

1.4.7.1 The fundamental molecule of photosensing

Although rhodopsin has been the name for the generic chromophores of vision since the mid 1800s, it was Wald who demonstrated in the 1930s that retinol was a primary precursor to the chromophores of vision and therefore a chromogen. Wald further proposed in the 1950s that the complete chromophore consisted of a protein opsin with a ligand retinol. **This chemical approach is not supported in this electrolytic model.** After fifty years, there has been no confirmation that rhodopsin can exhibit the spectral absorption characteristic of any of the chromophores of vision. Subsequent laboratory experiments have shown that retinol is not combined with the protein opsin within the inner segment of the photoreceptor cell. See **Section 4.6.2**. In addition, the rules of photochemistry and semiconductor physics dictate that the chromogen is converted into a different family of chemicals, the Rhodonines, that are the actual chromogens of vision. See **Chapter 5**.

1.4.7.2 The fundamental method of photosensing

Based on the retinol ligand proposal of Wald, Hubbard performed a series of in-vitro experiments involving cryogenic temperatures to develop a hypothesis describing photosensing as involving a complex series of chemical intermediaries. While these intermediaries may exist at cryogenic temperatures, the fields of quantum and semiconductor physics that were just maturing at that time strongly discount the existence of this same set of reactions at biological temperatures.
Lacking an understanding of the other options available via quantum and semiconductor physics, Hubbard proposed the excitation of the proposed rhodopsin involved a stereographic reorientation of the rhodopsin molecule in response to excitation by a photon. This approach provided the lowest energy event that approached but did not satisfy the requirement that the reaction could occur upon absorption of a photon. Three questions concerning this approach were never resolved. How this reorientation eventually generated a free electron was never demonstrated. Nor was it ever demonstrated how the modified molecule was returned to its original condition. Nor was the inability of a photon to provide the required energy ever resolved.

In support of the Wald-Hubbard proposals, Collins and Bownds, working in the same laboratory, attempted to support their hypotheses. Collins first promulgated the proposal that the retinol ligand was attached to the protein via a Schiff-base that was the lowest energy coupling provided by conventional chemistry of the time. However, this approach had "energy problems." Additional efforts were made to strain the arrangement of the molecule and its intrinsic charges to generate a lower energy requirement for excitation. These never bore fruition by predicting the absorption spectrum of the chromophores. As science continued to mature, Bownds attempted to find the binding location of the putative Schiff-base in his PhD thesis. This led to his publication, never pursued by him or the Wald school after 1967, of the hypothesis that the Schiff-base interfaced with the protein. The wording of his conclusion is significant. After using various procedures to digest the presumed chromophore, he said: "The smallest peptide of this nature also had a free N-terminal residue which was not lysine, indicating that the retinyl group must be attached to an internal amino group. This is presumably the ε-amino group of a lysyl side chain."

These mechano-chemical-stereographic approaches are not supported in this electrolytic model. Each of the above hypotheses can be characterized by a lack of confirmation, by their originator or an independent laboratory, over a span of forty to fifty years. Instead of a complex series of chemical reactions and isomerisms leading to the creation of a charge due to a photon, **Chapter 5** shows how the Rhodonines react directly to illumination. A photon causes a simple excitation of an unpaired electron associated with an oxygen atom of the Rhodonine molecule when in the liquid crystalline state. In accordance with conventional photochemistry, the excitation energy profiles of the Rhodonines are shown to represent the absorption characteristics of the visual chromophores precisely (including the ultraviolet chromophore used by many animals).

1.4.7.3 The fundamental method of charge generation by the photoreceptors

No theory of how rhodopsin participated in the generation of an electronic signal within the neural system emerged until the 1970s. Then, conceptual theories began to emerge that prophesied ionic gates in the putative plasma membrane enclosing the outer segment of the photoreceptor cell. The existence of these gates was supported primarily on kinetic grounds. They were based on calculations of the concentration of ions on each side of the putative membrane (in the absence of any boundary layers). Initially, these theories focused on the movement of simple ions, primarily Ca^{2+}. Recently, the emphasis has turned toward a complex protein, cyclic guanosine 3',5' monophosphate (cGMP) as the messenger ion that crosses the membrane and causes a change in potential. No specific mechanism by which rhodopsin directly controls these putative gates has been proposed. **This quasi-chemical approach is not supported in this electrolytic model.** This is due to a variety of reasons. Recent experimental research using high magnification electron microscopy has failed to prove the existence of a plasma membrane surrounding the outer segment associated with the photoreceptor cell. Lacking a putative membrane, whether there are gates present becomes moot. See **Chapter 4**. Conventional semiconductor physics provides a much more direct method of generating a free electron from the de-excitation of an excited Rhodonine molecule. This mechanism predicts the specific generator waveforms associated with the pedicle of the photoreceptor cells and measured in the laboratory. See **Section 4.7** and **Chapter 5**.

1.4.7.4 The fundamental method of potential generation within an axon

The Hodgkin & Huxley school developed their theory of neuron action during the 1960s based on the assumption that changes in electrical potential within a neural cell were due exclusively to the physical movement of ions through the cell wall. To support their theory, they proposed an ion pump located within the plasma membrane. Such an ion pump has not been further defined during the last fifty years. **This approach is not supported in this electrolytic model.**

In this work, the neuron is shown to consist of a series of individual conduits, each exhibiting a characteristic average potential compared to the exterior surround. An appropriate model of the neuron must account for both the average and signal related potential exhibited by each of these conduits.

If one begins with Gauss's law of electrical potential, and accepts the basic laws of semiconductor physics that apply to all materials, an alternate model for neural action evolves. This model only depends on the transfer of electrons through the bilayer membranes of the cell. This flow of electrons (and holes, the technical name for a counterflow of electrons) provides a much simpler explanation of the neural process than the ionic-flow hypothesis. It does not require a conceptual ion pump. The flow of electrons through the biological bilayer membrane is a fundamental mechanism of the electrolytic (as opposed to the ionic) theory of neural action.

The electrolytic theory of neural action leads to the definition of the biological transistor, the Activa, introduced in this work (**Chapters 8** & **9**).

1.4.7.5 The fundamental method of changing the potential of an axoplasm

The Hodgkin & Huxley school and subsequent investigators have relied upon the flow of ions through a membrane (quantifiable as a change in the conductance of the membrane) to cause a change in axoplasm potential. **This approach is no longer compatible with our knowledge of the axon membrane and is not supported in this electrolytic model.** As above, an equally plausible explanation of the change in potential of the axoplasm is the result of electrons passing through a sandwich of membranes biased to cause “transistor action.” Such a sandwich of properly biases membranes is defined as an Activa. This device and its associated mechanism completely account for the voltage change of the axoplasm as presented in **Chapter 8** and the **Appendices**. The mechanism is known as transconductance as opposed to the earlier envisioned conductance. It cannot be achieved by a single membrane. In this model, the only change in the conductance of the plasma membranes of a cell is due to the change in potential across the membrane acting as an electrical diode.

1.4.7.6 The fundamental mechanism of signaling between neurons

The field of neuroscience has not yet developed a quantifiiable method of signal transmission for inter-neuron or intra-neuron signaling. The current concept of inter-neuron signaling relies heavily on the recognition that many chemicals of the glutamate family are found near synapses. Based on this fact, and the inclination to employ chemical principles based on the education of most of the investigators, the concept of chemical neurotransmitters has been highly developed. Adherents to an alternate electrolytic concept of inter-neuron signaling have established a minor position within the field over the years. No substantive hypothesis concerning intra-neuron signaling has appeared in the literature although some electrophysiological mapping of potentials within a neuron has been

presented. **This chemical approach is not supported in this electrolytic model.** With the discovery of the biological mechanism underlying intra-neuron signaling, the Activa, it also became obvious how inter-neuron signaling is accomplished. These findings have led to the explicit description of the major mechanisms of signaling within the neural system. These mechanisms are fundamentally electronic (See **Chapters 8** & **9** and **11 through 15**). Because of these findings, it has become possible to definitize much of the operation of the visual system and to provide a new level of precision in presenting the descriptors of visual performance (See **Chapters 16** & **17**).

1.4.7.7 The fundamental mechanism of signal propagation in long axons

This work introduces a new concept to neuroscience regarding the transmission of signals over long axons. This involves the propagation of electromagnetic signals via the insulating wall of the conduit rather than the conduction of signals through the electrolyte of the conduit. This mode offers a speed advantage of several orders of magnitude. It is this mode of propagation that is the main reason for the existence of action potentials within the neural system.

1.4.7.8 The fundamental mechanism of achromatic and color vision

Beginning with the dawn of the 20th Century, a battle has raged between those inclined toward the Young-Helmholtz school and those inclined toward the Hering school of vision. The Young-Helmholtz school adopted the position that color vision was based on additive color principles as known to the artistic community of the time. Simultaneously, the Hering school embraced an opponent theory, employing what has become known as the principle of subtractive color. The additive color approach has been explored at great length under the assumption of linearity in the visual system, and been memorialized in a series of CIE standards based on a non-real Standard Observer. However, neither approach has provided precise answers to sophisticated problems in colorimetry. **Neither of these conceptual approaches is supported in this electrolytic model.** By analyzing the actual signal flow within the visual system, this theory shows that the fundamental signaling architecture of vision employs parallel paths. Further study shows that the photoreceptors perform a logarithmic conversion of all signals from a current, proportional to the incident photon flux change, to a voltage (See **Chapter 12 & 13**). The summing path provides an achromatic signal that is faithfully described by the luminous intensity function of vision under all conditions of illumination (See **Chapter 16** & **17**). Note carefully. These functions are not the functions promulgated by the CIE. The CIE functions are only obtained by smoothing the theoretical (and also measured) functions. The differencing paths, there are two in humans, generate two chromatic signals that are faithfully described by a New Chromaticity Diagram for Research (See **Chapter 17)**.

1.5 Focus of this Work

The initial focus of this work was on the human and possibly the mammalian eye. However, as the vision process unfolded while reviewing the literature, a set of underlying principles and techniques was recognized that applied to all the eyes found in nature. Although the variety of eyes and their optimizations are quite intriguing to explore, there are easily tracked evolutionary paths. Because of this situation, this work has expanded to include, codify, and explain many features common to all eyes in the animal kingdom. This broader scope, in line with the discussion on modeling above, has led to a better understanding of human vision because it has surfaced relationships present in the warm-blooded animals that can only be explored in cold blooded ones. A specific example involves the dependence on temperature of what is frequently called the generator potential of vision. This dependence is difficult to determine *in-vivo* in warm-blooded mammals but must be recognized during serious *in-vitro* experiments.

The previous published state of the art in neuroscience was inadequate to support the needs of this work. A new Theory of the Neuron was necessary. Such a dissertation is presented in **PART C**. Although this Theory will appear radical to many, its ability to explain the operation of the nervous system in animals is compelling. The crucial point is that the nervous system is based on electrolytic principles analogous to those of man-made electrical systems and the synapses (and other junctions) are primarily electronic in operation.

Whether one considers the retina a part of the brain or not, its complexity is accounted for by the level of signal processing accomplished within it. At least the architecture of this processing must be understood if vision is to be understood. This necessity led to a great deal more analysis being performed on the neural portions of the eye than originally planned. It included the detailed description of the signal amplification and signal processing functions in the retina. This amplification and processing are mediated by biologically based transistors (liquid-crystalline semiconductor devices) not unlike their solid-state semiconductor brethren. The paradigm shifts associated with this work compared with the conventional wisdom in the neurosciences will surely cause pain to the peer reviewers in that field. However, the success of the biological transistor concept in explaining how signaling is performed in the eye cannot be denied.

1.5.1 This Theory

The Theory contained in this work, the Processes of Biological vision, ***makes no assumptions about how the overall process is performed***. It relies entirely on the analysis of data obtained over the years by a large group of investigators. Making judgments between which data is valid and useful, and which data has missed the mark, has been necessary. However, usually, this judgment can be made expeditiously and without difficulty from the overall model and the large scientific base available in the literature. Frequently, it is possible to show why an investigator missed the mark by examining either the design or the tools of his experiment. As indicated below, where significant holes existed in the database, it was necessary, as with the neuron, to expand the scope of the investigation. This expansion was aimed at developing the necessary relationships from the more basic data available in adjacent scientific fields. The intent of this work has always been to make no assumptions, only to interpret what the basic data is portraying.

The Theory is the foundation upon which the models have been created. These models are useful in interpreting that theory and relating it to the database.

1.5.1.1 The purpose of this work

The purpose of this work is;

+ to provide the most thorough and comprehensive explanation of the visual process available in one place

+ to present the above explanation such that
  ++ it can be subdivided into individual subsections in the interest of further, more detailed, research

  ++ where necessary, it can be easily corrected based on new well designed and implemented experiments or on older, previously unrecognized, data

The author recognizes that the complexity of this work and the number of different disciplines involved will lead to misunderstandings based on different interpretations and possible errors in the work. The author welcomes any discussion or communication about the extension and perfection of the Theory and Model incorporated herein, especially if new results are available based on more highly controlled experiments. Since it is a principal goal of this work to maintain a high degree of mathematical rigor, it is extremely important that any proposed modifications to the work not involve “floating models” or philosophically oriented conjecture.

1.5.1.2 A synopsis of the models developed in this analysis

Taking a position with respect to other theories of vision is not the intent of this work. They are discussed only to compare them with the more rigorous framework of this work. The model of this work, which is inherently tetrachromatic and logarithmic, can be summarized mathematically in a Matrix Theory. It can also be reduced to a trichromatic form. Although still more sophisticated, this trichromatic Matrix Theory can be compared to the earlier Zone Theory of color vision in humans (See **Section 1.3.2.1)**

Several top level diagrams have been developed as part of the overall work of this investigator.. They are introduced as they are needed throughout the work.

- The *Top Level Block Diagram* of interest is presented in the following paragraphs of **Section 1.5.1**.
- A *Functional Block Diagram* associated with the initial stages of the visual modality as defined with respect to the Top Level Block Diagram appears in **Section 1.5.2**.
- The *Top level Schematic* is presented in **Section 11.6.1**.
- The *functional diagram* of major interest is presented in **Section 15.2.5**
- A Top Level Stage Diagram is presented in **Section 1.5.1.2.2**.
- A more detailed *Top Level Stage Diagram* , overlaid with *Top Level Operating Modes* appears in **Section 19.8.1**.

1.5.1.2.1 The Matrix Theory of this model

The proposed Matrix Theory is distinctly different from the previous Zone Theory. Whereas the Zone Theory was a theory of color vision, the Matrix Theory applies to all aspects of vision. Whereas the Zone Theory was based on fixed coefficients (derived at a nominal illumination level), the Matrix Theory employs coefficients describing the state of adaptation of the visual system. Whereas the coefficients of the Zone Theory were fixed and shared between the luminous and chromatic channels, the coefficients of the channels of the Matrix Theory contain two components. The fixed components are totally independent of each other. The second components are related to the state of adaptation of each spectral channel.

The Matrices of this model are derived directly from the physiology of the visual system. This form is illustrated in the figures of **Section 1.8.2**. [**Figure 1.8.2-2**] shows the presence of the individual spectrally selective photoreceptors of the trichromatic eye on the left. **Chapter 17** will present a similar figure for the tetrachromatic eye. Each photoreceptor contains an adaptation amplifier and a distribution amplifier. The adaptation amplifiers contribute the variable component in the coefficients of all of the matrices of vision. The signals from the distribution amplifiers appear at the pedicles of the photoreceptors. From there, they travel over various paths to each signaling matrix shown by the triangles on the right. Each of these paths controls the fixed component of the coefficients described above.

Four specific matrixing amplifiers are shown in the above figure. The upper two create the two chrominance signals passed to the brain. The third creates the brightness channel and the fourth forms a major node of the Precision Optical System that controls the motion of the eyes.

The matrix equations of the Matrix Theory involve logarithms and integrals, and are time dependent. They will be shown to apply to any state of the visual process without any approximations. The brightness channel describes the precise mathematical form of the (unsmoothed) Luminous efficiency function. Following smoothing, it describes the luminous efficiency function adopted by the C.I.E. under photopic, scotopic and mesotopic conditions.

Incorporating an achromatic photoreceptor signal channel in this theory has not been necessary. It will be shown that no creditable data exists supporting the existence of such a signal channel. The so-called scotopic and photopic visual functions in human vision are completely defined mathematically using the output of the brightness matrix. See **Section 17.2**. This output is calculated using only the inputs from the three chromatically selective photoreceptor channels. These channels are usually defined as the S-channel, the M-channel and the L-channel.

The signals in the two chrominance channels, created by the first lateral matrix, will be shown to cause the perceived colors of vision under all conditions. These colors can be described precisely in a Munsell color space (that is much larger than the normal Hering space). See **Section 17.3**.

1.5.1.2.2 The physiological model underlying the Matrix Theory

The proposed Matrix Theory is both physiologically based and separable into independent stages. As suggested in the Zone Theory, the visual system contains more stages than outlined there. These stages can now be defined in detail. An initial list is given here to show the scope of the individual stages in the visual system. However, the main text will develop the fact that the foveola of the retina and the remainder of the Precision Optical System operates separately from the remainder of the visual system. Thus, a more complex diagram is required to describe the complete visual process. These diagrams will be presented in **Section 1.5.2** and in greater detail in **Chapters 15, 16** and **17**.

Figure 1.5.1-1 shows the Top Level Block Diagram of the nervous system with a focus on the visual modality.

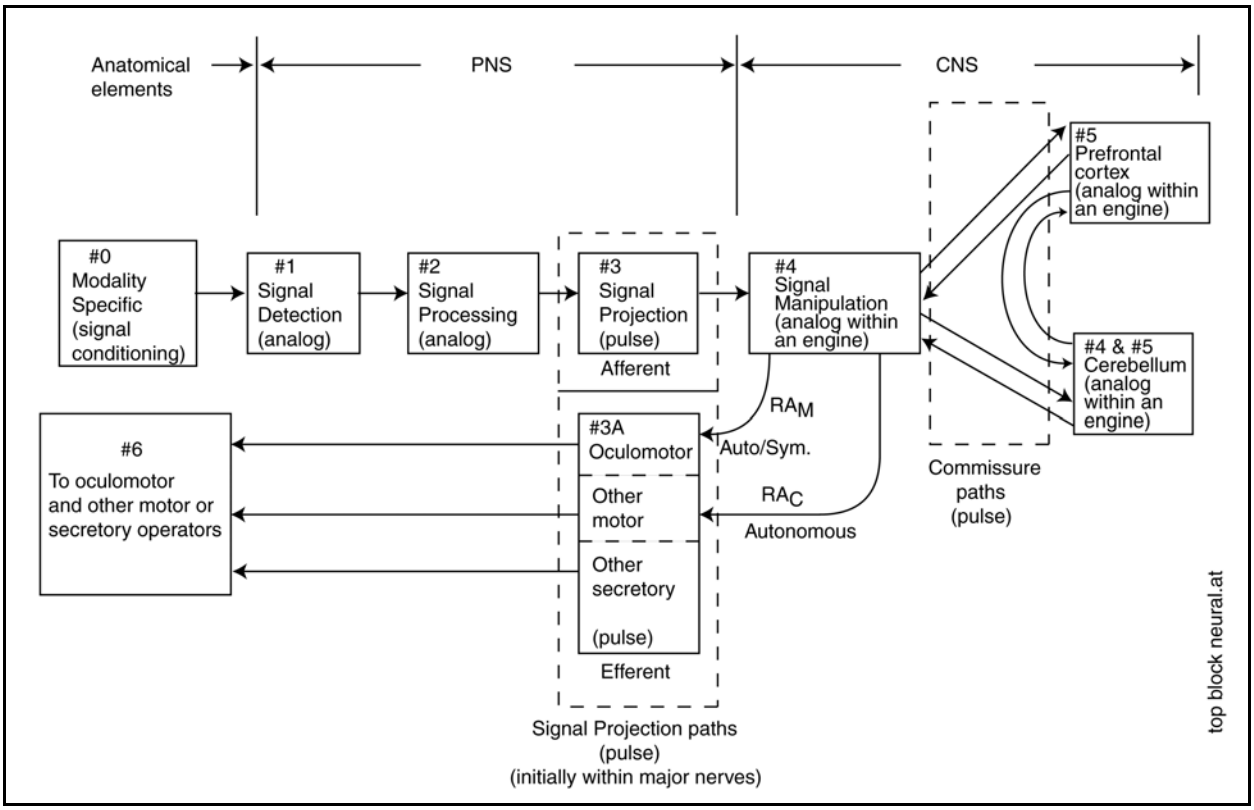

Figure 1.5.1-1 Top Level Block Diagram of the visual system developed in this work ADD.

Confirming that the output of the above matrices, found in Stage 2 of the Matrix Theory, are correct is not possible without understanding the remaining processing. Furthermore, the operational performance of the visual system, at least in the higher chordates, cannot be fully understood without defining and analyzing additional stages.

Defining three additional stages after stage 2 and one stage before stage 1 is desirable to satisfy these needs. However, maintaining some continuity with the previous database is desirable. Rather than renumbering the stages, the model of this work and the Matrix Theory will be subdivided into six stages beginning with stage 0.

The following functional stages complete the previously defined signalling environment of the visual system.

Stage 0 Genesis and metabolic support
Stage 1 Signal detection
Stage 2 Signal manipulation (in the retina)
Stage 3 Signal projection
Stage 4 Signal manipulation and perception (in the brain)
Stage 5 Oculomotor feedback servomechanisms

As indicated above, even this nomenclature does not account for the physiological optics stage, stage B, of the previously defined optical environment. It also fails to describe the transition of the visual signal paths from the linear mode to a star-type mode of interconnection as they approach the higher cognitive centers of the brain (See **Chapter 15**).

Ditchburn described stages B through 3 explicitly in 1973 and implied the activity of stages 4 & 5[150].

The complete Matrix Theory is tetrachromatic and based on the actual spectral absorption characteristics of the four (UV-, S-, M- & L-) chromophores of vision. It does not rely upon any synthetic expressions such as tristimulus values.

Except for the closed loop nature of the Precision Optical System, the visual system is free of external feedback until the cortex is reached. Within the cortex, even the modes of signaling defy complete description at this time. The closed loop operation of the POS will be developed in detail in **Section 7.3**.

To evaluate the Matrix Theory more completely, the cytological mechanisms of vision must also be introduced into the model.

1.5.1.2.3 The photochemical foundation underlying this model

Application of the rules of conventional photochemistry leads to a detailed understanding of the photosensing mechanisms of vision. Comparison with the relevant analog in silver halide chemistry shows how Vitamin A (retinol) can be modified to create a family of four chromophores. These chromophores exhibit precisely the absorption spectra of the visual chromophores. The resulting family of four Rhodonines can be described as retinines. Their structure can be described by a variety of chemical terms. They are polyines. They are members of the indicator family and each can be described as a carboxyl-ion system. To achieve the required absorption, the Rhodonines must be adsorbed as a liquid crystalline coating on a semiconductive substrate.

To satisfy the dietary requirements of all of the families of the phylogenic tree presented above, the Vitamin A used as a chromophore may be in one of three forms. It may be Vitamin A_1, Vitamin A_2 or Vitamin A_3. The type of Vitamin A does not affect the spectral response of the chromophores significantly. All of the Rhodonines exhibit peak spectral absorptions at 342, 437, 532 or 625 nm (with only slight variations with temperature). The widths of their spectrums are determined by the unique arrangement of the adsorbed coatings on the disks of the Outer Segments of the photoreceptor cells.

The details of both the photochemistry and the structural arrangement are presented in **Chapters 4** and **5**.

1.5.1.2.4 The Electrolytic foundation underlying this model

Contrary to the conventional wisdom, signaling within the neural system of animals is not chemically based. **The signaling function is electrolytically based.** The electrolytic hypothesis has provided answers to questions that cannot even be expressed under the chemical hypothesis.

The neural system consists of a vast array of signal paths built from a basic set of components. These components are electrolytic conduits (in place of metallic wires) separated by Activas, active electrolytic semiconducting devices (in place of man-made transistors). They are powered by electrostenolytic sources based on the glutamate modification of the Krebs cycle. This cycle is used throughout the animals body as a source of energy.

By accepting the data showing that the neural system of the animal is electron-flow based, as opposed to ion-flow based, moving beyond the conventional wisdom is possible. It becomes possible to define completely the analog and pulse signals found in the retina of the eye and to show how they are generated and manipulated.

The electron-flow model provides a straightforward description of the illumination level dependent and time dependent effects involved in vision. These effects involve depletion of the available current supply sources to the semiconductor amplifiers present and in this way relate to the metabolic materials close to the photoreceptor cells.

The electrolytic model also eliminates the need to search for the elusive ion pump postulated in the ion-transfer-based approach. It also becomes possible to describe the simple functional characteristics of the synapse without hypothesizing complex cascades of chemical reactions.

This model has provided a much simpler explanation of the phototransduction process then:

+ the proposition that rhodopsin creates an output signal through isomerism.

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[150]Ditchburn, R. (1973) Eye-movements and visual perception. Oxford: Clarendon Press page 268

+ the proposition that a putative “glutamate cascade” provides amplification of the above signal.

This model should be looked upon as a comprehensive electronic model. If another comprehensive model gives equivalent results, using it under selected circumstances may be more appropriate. However, the investigator should be wary of isolated “floating models” that are not supported by or do not contribute to a comprehensive overall theory/model.

1.5.1.2.5 The molecular foundation underlying this model

The Theory addresses a variety of subjects at the molecular level and the model must reflect these situations. One of the most important is coincident simplification of the local structure of the membranes of a cell and their differentiation into individual zones. The membranes of a cell are made up primarily (more than 90% by weight) of two lipid bilayers with their hydrophobic surfaces in close communion. When the two lipids are symmetrical, the membrane forms an excellent electrical insulator. The lipids are frequently asymmetrical[151]. When the lipids are asymmetrical, the membrane forms an excellent electrical diode. The asymmetrical regions of the membrane are important sites of charge transfer between the sides of the membrane. These sites play a variety of roles in the neurological process.

The asymmetrical regions of membrane abutting other regions of asymmetrical membrane in adjacent cells (conduits, see later) can form active semiconductive devices, Activas, between those cells (conduits). These devices can provide a very low impedance signaling path between neurons.

The asymmetrical regions can also provide electron conducting paths between the two sides of the membrane. Normally, these membranes are reverse-biased and form an effective barrier to current flow. However, if the surface of the membrane is coated with an electrostenolytic material, current can be injected into the cell to create the negative potential normally associated with chambers within a cell.

As described in the previous section, the glutamates provide the primary source of electrical power to the neural system. GABA, the glutamates and glycine are present as part of a glutamate cycle (a variant of the Krebs cycle) and are the principal materials coating the above asymmetrical regions of cell membrane. See **Section 7.7** for details.

1.5.1.3 A synopsis of the results of this analysis

There is a complete synopsis of this work on the website, www.4colorvision.com/files/synopsis.htm or as part of the front matter of the published work. To provide a stand alone document, this PDF version of the work contains an extensive summary of the findings in **Section 1.9.** The website version will always be the most contemporary.

1.5.2 This Model

The work presented here attempts to go back to basics and conform any measured data to a model supported by rigorous concepts and the mathematics appropriate to those concepts.

In some (many) cases, this leads to the generation of new concepts not currently found in the vision literature. Before proceeding, these concepts are tested against the measured data in the literature. Usually, this requires comparison of data from a variety of investigators and animals. The concept is then adopted, modified or if necessary, abandoned in favor of a more basic one. It is not modified on philosophical, heuristic or political grounds. If the concept explains the data and can be supported mathematically, it is adopted.

In the more highly evolved animals, the complexity of the computations and interconnections related to the signals created by the initial photoreceptor cells and passed to the cortex of the brain is great. Techniques were sought that alleviated the problem of analyzing these signals as much as possible. This was done by concentrating, in the higher mammals, on the signal paths associated with the photoreceptor cells at the confluence of the line of fixation and the retina. The literature claims that typically, these photoreceptors have individual signal paths directly to the cortex of the brain.
It will be shown that this is probably true. Adopting this claim does allow the rigorous definition of the output (action spectra) of an animal as a function of the input illumination when adequate parametric control is maintained

[151]Miljanich, G. et. al. (1979) Disaturated and dipolyunsaturated phospholipids in the bovine retinal rod outer segment disk membrane. *Biochim. Biophys*. Acta. vol. 552 pp 294-306

during the experiment.

The correlation of data from different species, and usually different investigative teams provides many valuable insights and corroborations.

During the formulation of this work, it became clear that the human visual system is not the most highly developed in the animal kingdom. This may come as a surprise because of our normal homocentric tendencies and the considerable sophistication of the human eye compared with man's capability to reproduce such an eye in the laboratory. However, the human visual system clearly;

+ does not achieve the on axis resolution of some birds

+ Cannot detect or process polarized light signals as do most insects

+ Cannot detect light in four different spectral regions at once, including the ultraviolet, as can many vertebrates and other classes.

+ does not have a nictating lens to support a rapid transition between an aquatic and a terrestrial existence as do some mammals and birds

+ Cannot change the operational mode of the eye from an imager to a motion detector as can many hunters, especially in the cat family.

It also became clear that the animal visual system has evolved from and remains inherently a change detection system. As is easily shown, without either a temporal or spatial change in the scene, the human eye provides no output signal (leaving the person blind). Change of some sort is absolutely required between the target in the field of view and the line of fixation of the eye. To achieve imaging of the entire scene, there must be motion of the whole scene relative to the line of fixation. The key to the imaging capability of the human eye is related to the constant small angular oscillation of the line of visual fixation (tremor). Lacking this oscillation, the person only sees "flashes" and "shadows."

The purpose of this work is to put the above and many other specific effects into proper conceptual and mathematical context.

1.5.2.1 Tree of Deviations between the Electrolytic & Chemical theories of vision

Figure 1.5.2-1 provides a brief comparison of the foundation of this work, The Electrolytic Theory of Vision compared with the "conventional wisdom" concerning the process of vision *in animals*. *Homo Sapiens* is a subset of this set.

Area	Conventional Wisdom	This Theory	Comment
Theory of Color Vision	Trichromatic	Tetrachromatic	UV unknown in early 1800's
Optics	Spherical (Gaussian)	Elliptical (thick lens)	With field lens added
Neuron Operation	Biochemical	Electrolytic	
Active device in neuron	<Unknown>	Activa (liquid crystal)	A Major Discovery
Class of Sensor	Static Imager	Change Detector	Imager is emulated
Sensor types	Rods & Cones	One functional type	Morphology irrelevant
Phototransduction	Complex	Simpler	See text
Photo-excitation	Photoconductive	Quantum-mechanical	
De-excitation	Enzymatic	Exciton/electron transfer	
Location	OS "membrane"	Microtubules in disk stack	
Active chromophores	Rhodopsins (proteins)	Rhodonines (retinoids)	Defined @ molecularr level
Role of Opsin	Part of photoreceptor	Passive substrate	
Role of retinol	Part of photoreceptor	"seed" for Opsin	
Transducer location	Internal to sensory n.	External to sensory n.	Electron micrographs
Transducer state	Liquids & solids	Liquid crystalline	
Polarity of sensor outputs	Two types	One type	
Amplification in neuron	Chemically based	Electronically based	See text
Amplification mecanism	"Chemical cascade"	Transistor action	
Method	Pores in membrane	Integral to membrane	See text

Tree of deviations.ai

Figure 1.5.2-1 Tree of Deviations between chemical and electrolytic theory of vision. Part 1 of 2. See test for brief discussion before following citations to specific discussions in later chapters.

Each category in this figure will be addressed extensively in later sections. Only a few comments will be given here. The conventional tri-receptor theory of color vision (derived from and applied to humans) is usually attributed to Young in 1802-03. At the time, ultraviolet light was virtually, if not completely unknown. An aphakic human eye was unknown except because of a serious injury or birth defect. The literature is full of references and data applying to *tetrachromatic* vision in many types of animals, including aphakic humans.

Area	Conventional Wisdom	This Theory	Comment
Signal Processing	Assumed linear	Highly nonlinear	Hybrid in character
Adaptation Function	<Unknown>	Bleaching of chromophores	
Signal process. mech.	Inhibition	Subtraction	Simple differencing
Luminance	<Undefined>	Sum of Logarithms	
Chrominance	Linear Addition	Difference in Logs's	A key difference
Signal feedback	Assumed external	Primarily internal	See text
Temporal filters	Mutipole, lumped	No mulipole filters	Variable bandwidth
Signal transfer	Chemical junctions	Electronic (Gap) junctions	
Location	Synapses	Synapses, NoR, internal	Synapses are active
Signal Projection	<Not addressed>	Stage 3 pulse circuits	
Type of signaling	<Not addressed>	Monopulse oscillators	
Code used in Signaling	<Unknown>	time-delay phase modulation	IRIG standard
Action Potential forming	<Unknown>	Regenerative amplifiers	
Signal Perception			
Shift in White Point			
Object space	<Unknown>	Differential adaptation	
Perceptual space	Speculative	Does not occur	
Contrast sensitivity			
No relative movement	< not addressed>	No vision (blindness)	3 Hz high pass filter
Initial dynamic range		~ 200:1	Limited internally
Color "Primaries"	3, equilateral triangle	4, rectilinear	Rationalizes Hering & Helmholtz

Tree of deviations2.ai

Figure 1.5.2-2 Tree of Deviations between chemical and electrolytic theory of vision. Part 2 of 2. See test for brief discussion before following citations to specific discussions in later chapters.

The gap junction, found between neurons, *and within neurons*, is the key to the operation of the nervous system. The parameters of this gap and the adjacent cell walls define an active electrolytic semiconductor device. This device provides the explanation for how the sensory and signal processing neurons of vision work.

An unexpected consequence of attempting to develop an overall model of the visual process was the realization that the neuroscientific community could not provide a mathematically valid transfer function for the neurons used in vision. This problem has been exacerbated by two conditions;

+ the failure of the community before 1970 even to admit the existence of an electrical interface between sequential neurons in a system, now awkwardly but accurately called a “gap junction.”

+ the failure of the community before 1970 to accept the presence of neurons in the retina, and other sensory cells, operating in an analog mode, i. e., not involving pulse signaling (so-called action potentials)

Because of the above conditions, it was necessary to carry out a very extensive analysis of both the basic neuron and how multiple neurons interconnect. This analysis resulted in four major findings which will be presented in detail in a later chapter;

+ neurons operate exactly like any other semiconductor based electrical device

+ a single neuron may contain more than one active amplifying device

+ the active amplifying devices of a neuron are not intimately associated with the Soma of the cell.

+ Many chemical species found near a neuron are not related to the signal handling capability of the neuron but are related to the electrochemical task of providing electrical power to the amplifying device.

This last finding is critical to the understanding of the vision process. Its corollary is that the vision process is an electron flow based process. It does not rely on the flow of ions to generate a signal for ultimate transmission to the brain. This is particularly relevant to the current literature. It is attempting to show that the photoreceptor cell is critically dependent on the flow of several large ions to create the signal representing photodetection. It will be shown that these large ions are only used as solutes in a battery which powers the active device within the photoreceptor.

This model has been built on a broader base than just the data from the biological and psychophysical communities. It has drawn heavily upon the work of the photographic imaging community and the chemical industry involved in developing color photography. It also integrated many concepts from both the black and white and color television industries, and the burgeoning semiconductor industry beginning in the 1950's. The result is a mathematically rigorous model based on four foundation concepts:

+ that all biological vision has evolved from a common ancestor and uses the same fundamental mechanisms.

+ that biological vision is based on quantum-mechanical photo-*excitation,* an inherently electronic concept***,* and not photo-*isomerization,*** an inherently mechanical concept--i. e., a chemical rearrangement**.**

+ that biological tissue has an electrical impedance that is properly represented as a diode in series with a battery,

+ that the animal neural system is based on a biological transistor.

Each of these four concepts can be further divided into a series of Axioms. As an example, the first concept leads to the axiom that the retina of the chordate eye is structurally inverted compared with the arthropod and mollusc eye to provide freedom of rotational motion.

In addition, additional axioms can be defined based on various pairs of the above concepts. As an example, the last two concepts lead to the axiom that the signal processing function in vision uses ***a thermodynamically reversible process that does not involve the dissipation of power.***

A particularly important axiom can be derived from the last three concepts. This axiom states that the signal processing carried on in the retina and the cortex ***are based on exponential arithmetic*** and cannot be modeled properly using linear algebra.

- - - -

Figure 1.5.2-3 provides an overall functional block diagram for the processes of biological vision so that more detailed models can be developed and used to define more detailed relationships. This figure is an expansion of the previously presented global model. This diagram is drawn broadly to encompass all possible types of tetrachromatic animals. Because of that emphasis, it is more complex than the diagram required to document only the trichromatic vision of the Human. Although more complex and complete than any other known model, it is well supported by the literature and the discussion to follow. The visual process can be divided into a series of steps as suggested by the numbers from 1 to 18. These numbers provide a convenient way to focus on a particular function or relationship. The dual ultraviolet channels (UV_1 & UV_2) shown on the left are only found in *arthropoda*. In most members of *chordata*, there is only one ultraviolet channel. In humans, and other large chordates, the UV channel is present but its effectiveness is small because of the absorption of the UV component of light by the lens group. The figure is discussed in more detail in **Section 15.6.4**. Except for the lateral geniculate nuclei (step 14), the items included in the gray box and related to the diencephalon of the brain have not been included in most articles and texts related to vision. It is critical that the role of the diencephalon be understood if vision is to be understood. Note the large degree of redundancy in the system. The subsystem to the right of the step numbers applies only to the central 1-2 degrees of the visual field in humans while the subsystem to the left applies to the entire field of view. **Figure**

18.1.3-1 presents an additional variant of this figure that supports the unexpected functional requirements associated with the overall visual system. It also highlights the major failures of the system that lead to color-blindness.

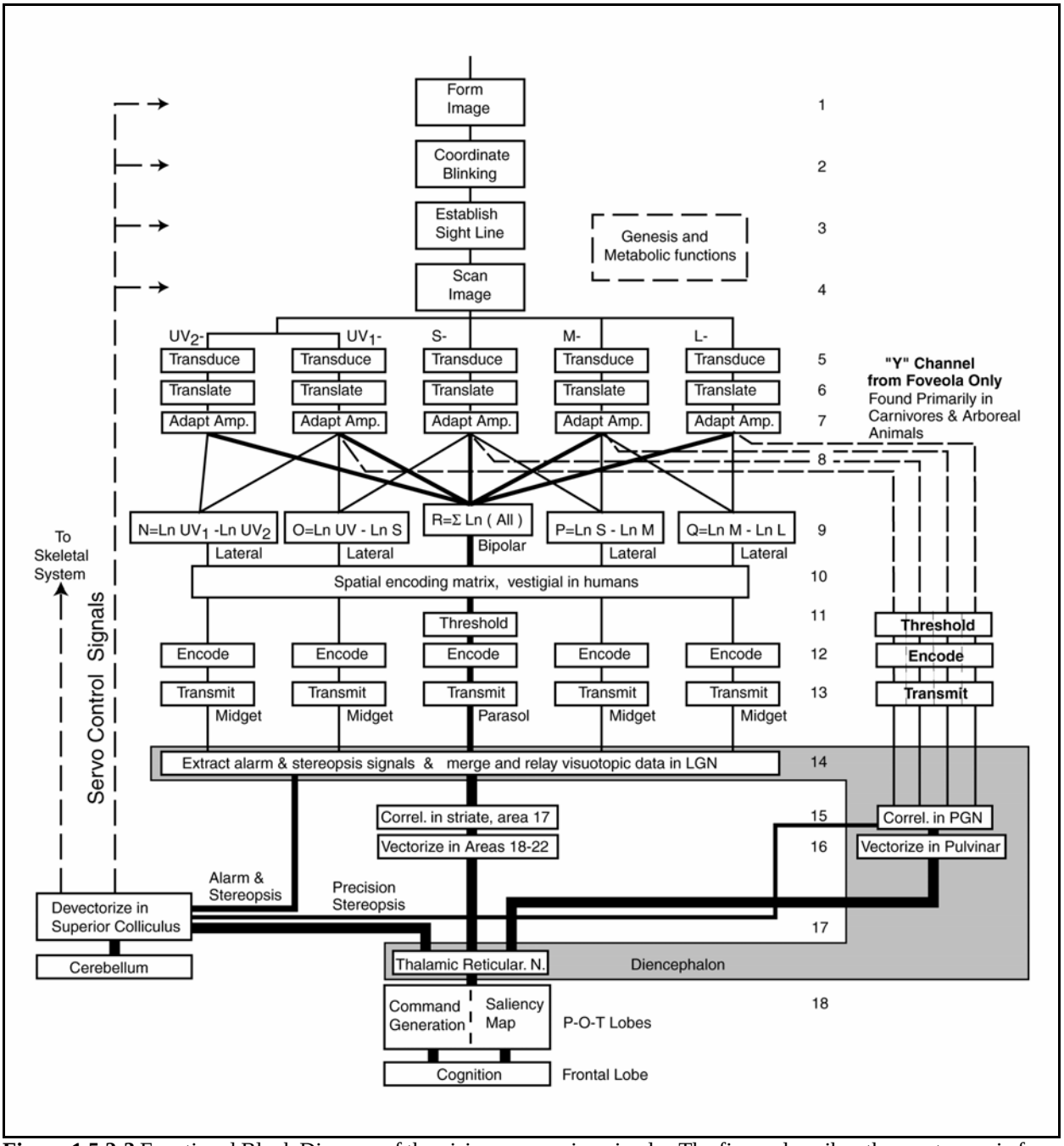

Figure 1.5.2-3 Functional Block Diagram of the vision process in animals. The figure describes the most generic form of tetrachromatic animal vision. It includes a variety of elements not found in the trichromatic visual system of Human. The numbers appearing vertically to the right will be used in later discussions. The narrow solid lines represent afferent signal paths that show a visuotopic relationship to the scene imaged. The dashed lines indicate efferent signal paths. The heavier solid lines below step 15 represent abstract signals that do not exhibit a precise visuotopic relationship to the scene. Neurons within these blocks do exhibit a receptive field that can be traced to broad areas of the field of view, but not on a one-to-one basis. The machine language (neural code) used to transmit signals below step 15 are unknown at this time. represent quasi-efferent signal paths containing signals that contribute to the final neuro-motor command signals. The dashed box represents additional critical elements of the visual system that support the visual system.

As suggested above, understanding the operation of the oculomotor subsystem of vision is critical if one is to understand the operation of the visual system. To accomplish this requires consideration of certain signal paths beyond the afferent signal paths leading to the brain that are normally considered. The definition of efferent and afferent neural paths becomes difficult when one is examining structures related to the brain itself. In this figure, the signal paths shown as dashed-dot lines are considered quasi-efferent signal paths for they are involved in command signal generation. These signals are collected to form the final efferent neuro-motor signals shown as dashed lines. These vision related efferent signals are created in the Super Colliculus (also described as part of the Tectum of some animals). The numbers along the right margin will be used later in this work to focus on specific functional areas. They will also be used in **Chapter 18** when discussing various anomalies in the operation of the visual system of man.

The figure has also been extended into the metabolic domain by the definition of Stage 0. This stage is concerned with the vascular system and several very critical metabolic processes. These involve the continual creation of the disks of the Outer Segments of the eyes, the creation of the chromophores coating the disks of the eyes and the supply of the power necessary to operate the neural system. This stage is introduced as the dashed box in the upper right quadrant.

The foundation for and details related to this model will be developed in **Chapter 11** and subsequent chapters in **PART D**.

1.5.2.2 The morphological eye from an electronic perspective

In a more physical context, **Figure 1.5.2-4** provides a schematic model of the vision process, using the morphological nomenclature of those investigating the human visual system. The fundamental feature of this figure is that the eye does not exist in isolation; it is an integral part of an overall platform that is in intimate communication with the brain. This communication involves both signals going to the brain and emanating from the brain. The eye is also supplied with metabolites via the vascular manifold that are absolutely necessary for vision. An inadequate supply of these metabolites can have many clinical consequences. Failing to recognize the role played by any of the functional features shown will lead to considerable difficulty in understanding the process of vision. As a simple example, when the brain instructs the eye to rotate to a new point of fixation, open loop commands are sent to both the eye muscles and the short term memory associated with vision. During rotation, the memory is blocked from accepting new visual information. Following the computed time required for rotation, the brain begins to acquire new imagery from the eye based on where it thinks the eye is now pointing. If the eye has failed to rotate properly, confusion will reign. Fortunately, the brain will usually attempt to correct this problem by sending out a second set of instructions to correct the differential error encountered.

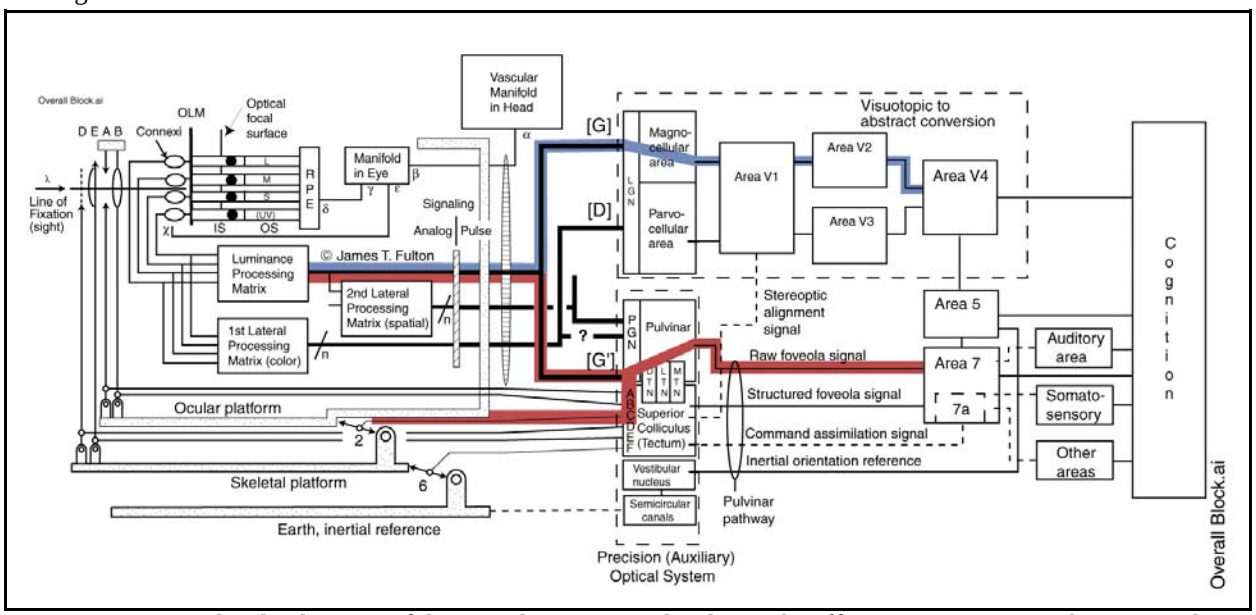

Figure 1.5.2-4 Top level Schematic of the Visual System in *Chordata*. The efferent nerves serving the eye are shown in light lines emanating from the Superior Colliculus. The afferent signal paths are shown by darker lines emanating from the photoreceptors. The darkest portion of these lines indicate the signal projection sub-system, the only parts of the afferent paths involving action potentials. See text for details

Figure 1.5.2-2 is quite complex and cannot be easily discussed without the development of more detailed submodels. These will be developed in the chapters that follow and culminating in **Chapter 15**.

A few points of explanation related to this figure are necessary here. The figure uses structural engineering symbols along the left and bottom edge to illustrate the mechanical elements and the three inertial platforms important to the eye. Each of these platforms is manipulated by a series of muscles. The muscles are shown by hollow circles associated with the tombstone shaped pillow blocks. The numbers next to the double ended arrows show the number of degrees of mechanical freedom involved at that location. A series of efferent nerve pathways connecting to these muscles is shown by light lines along the bottom of the figure. Neural paths labeled (C) and (F) represent groups of neurons supporting these muscles. These pathways are signal projection pathways, involving action potentials, supporting the musculature of the eye. Oyster[152] provides more detailed information about these efferent neural paths. He also discussed the non-signal afferent paths of the ocular globe associated with pain and tactile sensation (not shown here). The structures at the upper left are; (A) the iris, (B) the lens, (D) the eyelid, and (E) the nictating or second eyelid found in most chordates. At the top of the Chordate evolutionary path, this second eyelid is only rudimentary. It is well developed and highly important in many other chordates.

The incident illumination is shown by the arrow. This illumination is brought to focus at a point generally within an area of the retina populated by the Inner Segment (IS). Many of these IS have a roughly spherical element, shown by the black dots, that aid in collimating the illumination before it enters the individual OS elements.

The afferent signal paths in the eye originate at the photoreceptor cells. There are four sets of photoreceptors in the eye of *Chordata*, only three of which are normally used by man. Each set exhibits a different peak absorption spectral value. The sets are labeled L, M, S and UV to describe the individual chromophore present and the spectral band involved. L stands for the long wavelength, M the mid-wavelength, S the short wavelength and UV the ultraviolet centered wavelength of vision. The vast majority of the neurons in the eye, more than 95%, are associated with signal generation or signal manipulation and involve analog electrical signals. They are shown by heavier lines. It is only in the signal projection subsystem, including the ganglion cells of the retina and the initial decoding circuits of the cortex, that action potentials are found. Those signal paths exhibiting action potentials are shown by the heaviest lines in the figure but without further description.

The eye of Chordata is unique in the amount of signal processing carried out within the retina. It is of four distinct types. The brightness processing matrix accepts inputs from all of the photoreceptors in a given cluster of photoreceptors and creates a signal channel representing a wide equivalent spectral bandwidth signal. It outputs a single signal representative of each cluster of photoreceptors in the retina. The first lateral processing matrix is populated by horizontal neurons that extract information from the same photoreceptors and forms up to three orthogonal signals representing the chrominance information in the observed scene. The second lateral processing matrix is populated by amercine cells. While not significant in man, it is highly developed in many chordates. This matrix has responsibility for performing preliminary calculations regarding the spatial content of the signals associated with a given cluster of photoreceptors. All of the signals produced by these matrices are analog signals. They are received by the ganglion cells and encoded for transmission to the brain.

Toyoda, et. al. has described the above signals in some detail[153]. However, their early analysis was incomplete in defining the nature of the output of the amercine cells (what he included in his intermediate horizontal cells of the RGB type). These cells are found in the 2nd lateral processing matrix and their output is more complex that they reported. His L-type cells responded to luminance (hyperpolarized for S–, M– & L– inputs) and will be shown to be bipolar cells in this work. His RG-type cells corresponded to horizontal cells creating the Q–channel chrominance signals of this work. Some of his RGB-type cells may have corresponded to the horizontal cells creating the P–channel chrominance signals of this work.

The ganglion cells are the input elements of the signal projection system of vision. The signal projection system is designed to overcome two problems. First, the individual signals received by the ganglion cells still number in the millions. To support the high angular rates of rotation of the chordate eye, yet provide structurally reliable nervous connections to the brain, this number must be reduced. Second, analog neural signals cannot be efficiently transmitted long distances. The signal projection system of chordate vision is designed to overcome these problems. It accomplishes this using two additional types of signal encoding. One type is applied to all signals while the other is used selectively. The second technique recognizes that the eye supports a variety of function performed by the brain. The primary function supported by most of the eye is to perceive alarm signals, generated by the

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[152]Oyster, C. (1999) The Human eye. Sunderland, MA: Sinauer Associates, Chap. 5

[153]Toyoda, J-I, Kujiraoka, T. & Fujimoto, M. (1982) The opponent color process and interaction of horizontal cells *In* Drujan, B. & Laufer, M. The S-Potential, NY: Alan Liss

photoreceptor cells, as rapidly as possible. It is of primary importance that the occurrence of these signals be transmitted to the brain immediately. The importance of the amplitude of these signals above a threshold is less important. An equally important function supported by only the central part of the fovea, the foveola, of the eye involves the detailed scanning of a small scene for purposes of identification and recognition. This function only involves a few thousand photoreceptors.

When addressing the alarm requirement, the signal projection system encodes most of the signals (other than those in the foveola) from the various clusters of photoreceptor cells by their point of origination. It does this in the analog domain using a spatial encoding technique called n-ary encoding. This technique will be discussed later. The technique allows less than a thousand neurons in the optic nerve to transmit all of the initial (alarm) signals from a few million photoreceptor clusters along with an unambiguous address for each signal. The amplitude of these signals is subsequently carried over the same system. The signals from the foveola may be included in this encoding scheme. However, these important signals are also sent directly to the Pretectum of the brain without spatial encoding.

When addressing the distance requirement, the signal projection system treats all of the signals from the retina the same. It encodes them using binary pulses that are transmitted more efficiently. The type of encoding is carefully chosen to preserve the timing information associated with the alarm function. The timing of an initial pulse in any luminance signal is directly related to the time the analog signal exceeded a threshold value. This timing is extremely important to the brain in determining where the threat is relative to the entire body of the anima, not just relative to the eye. In the case of the signals from the foveola, this precise timing allows more precise analysis of the geometry of the threat. Additional information related to the alarm function is sent subsequently by time delay encoding. This encoding approach sends information about the highest contrast threats first. The higher the signal level, the shorter the time delay before the next pulse is sent. This type of encoding is also very helpful to the analysis of signals from the foveola.

All of the signal information is transmitted to the brain over the optic nerve. The basic plan directs the brightness information to the magnocellular portion and the chrominance information to the parvocellular portion of the Lateral Geniculate Nucleus (LGN). A division is shown in the brightness pathway. It suggests the brightness data associated with the foveola is sent to the Pretectum. This data path may consist of the raw signals from the individual photoreceptors. The same data from the foveola may also be encoded and sent to the magnocellular part of the LGN. The divide shown in the chrominance data from the first lateral processing matrix is more tentative. Whether chrominance data is computed and sent to the Pretectum from the foveola is open to question. Many psychophysical experiments have shown the analytical capability of the human visual system is not very good for test images containing chromatic differences but no luminance differences. This may be because the chrominance information is not sent to or used by the Pretectum. It is also possible that the test images were of relatively low chromatic saturation or poorly chosen compared with the spectral absorption bands of the eye.

Note the close coupling between the Pretectum and the Superior Colliculus. It suggests the fact that the signals from the foveola can be analyzed without the participation of higher cognitive centers. The process is complex and will not be discussed here. Only the results of the analysis need to be sent to the higher cognitive centers for purposes of recognition and further action.

A critical path in the operation of the eye involves the supply of electrostenolytic supplies to the dendrites of the photoreceptor cells. These supplies reach the dendrites via the Inter photoreceptor matrix (IPM) filling the space between the Outer Segments (OS) of the photoreceptor cells. The IPM is fed in turn from the Retinal Pigment Epithelium (RPE). The RPE obtains its metabolic supplies from the vascular system via the choroid vascular circuit labeled δ in this figure. The health of this vascular circuit is critical to the performance of the eye at widely different illumination levels.

The vertical ellipse drawn directly below the Vascular manifold represents the optic nerve. This element with its "global" name carries both the vascular supply to the eye and both afferent and efferent neurons supporting the visual system. The optic nerve is not a passive structure. It contains many Nodes of Ranvier that are active signal regeneration circuits. They are supplied metabolically by the vascular manifold labeled $\alpha-\beta$.

Figure 1.5.2-5 from Cowey & Stoerig[154] provides a more detailed schematic including additional nomenclature describing the signal paths from the retina to the central nervous system, CNS. As noted here, a signal path has long been described from the retina to a location along the brachia of the superior colliculus (SC). Most frequently, this location has been labeled the sensory (afferent) portion of the predominantly efferent signal handling superior colliculus because of early crude morphological investigations. Here, because of its importance, this morphological

[154]Cowey, A. & Stoerig, P. (1991) The neurobiology of blindsight *TINS* Vol 14(4), pp 140-145

structure between the LGN and the SC will be labeled the perigeniculate nucleus (PGN) to more closely associate it with its afferent sibling, the lateral geniculate nucleus (LGN). While the number of neurons in the optic nerve serving the PGN is smaller as indicated by the arrow width, 100,000-150,000 versus the number serving the LGN, one million per eye, the area of the retina served is smaller in the case of the PGN. The signals to the PGN only originate within the 1.2 degree diameter field known as the foveola centered on the point of fixation.

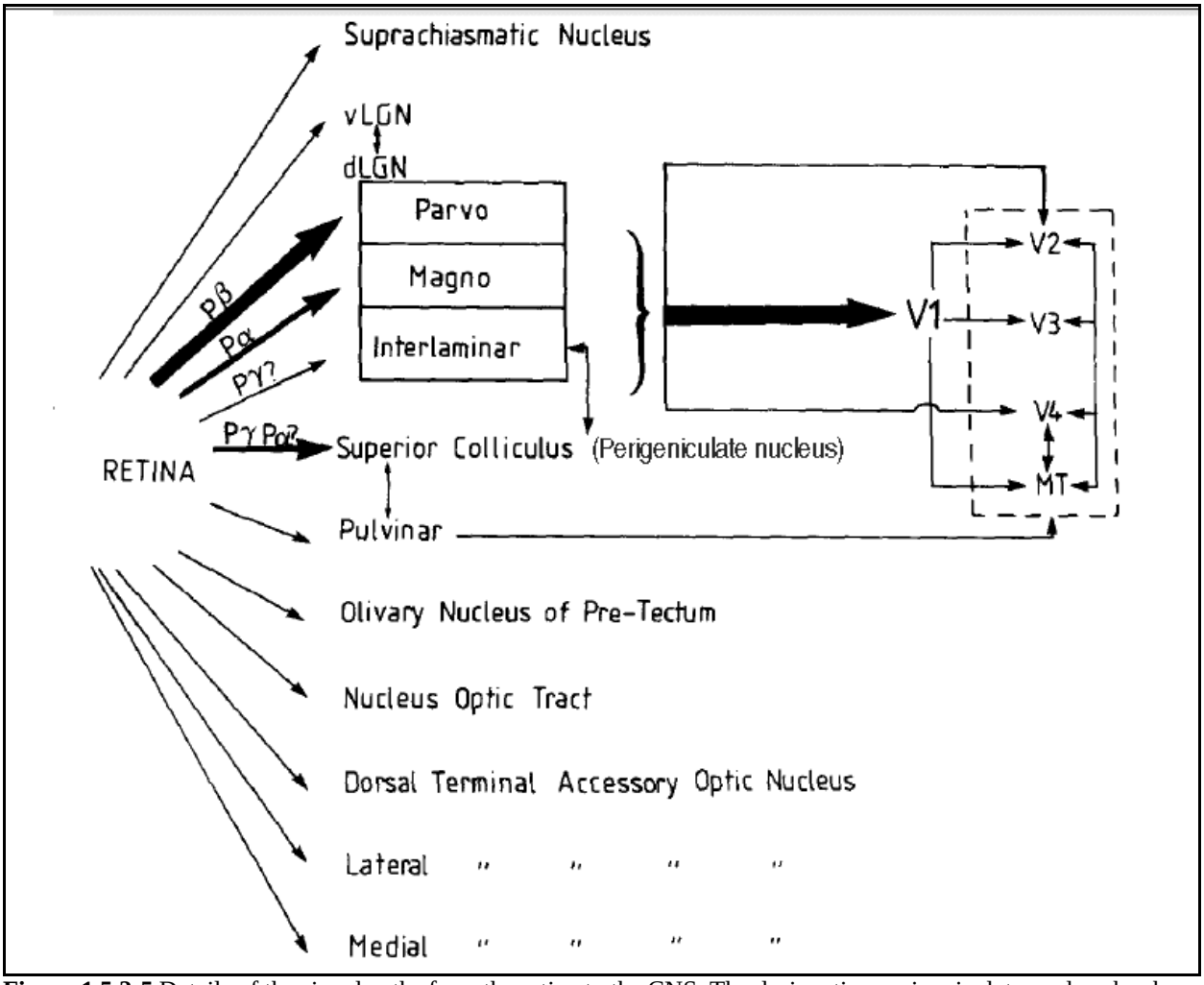

Figure 1.5.2-5 Details of the signal paths from the retina to the CNS. The designation perigeniculate nucleus has been added. The scheme excludes the extensive further connections between the initial cortical visual areas and the many further visual areas. The thicker arrows indicate the heaviest and most studied projections. The labels containing a question mark should be ignored. See text. Modified from Cowey & Stoerig, 1991.

The dual pathways of vision frequently suggested in the literature can be defined as the LGN-occipital pathway leading to the large area or scene processing areas of V1 through V4 and the PGN-pulvinar pathway serving the object recognition function areas within the pulvinar. Both pathways converge in the association areas near the intersection of the parietal, temporal and occipital lobes of the CNS. Here, the convergence is labeled the MT based partly on its original discovery in sensing motion. More generically, it is now labeled V5 or MT/V5.

The path labeled Pα consists of neurons carrying encoded brightness information (the R–channel of this work). The path labeled Pβ consists of neurons carrying encoded chrominance information (the O–, P– and Q– channels of this work). The path labeled Pγ is poorly defined at this time. The neurons proceeding to the PGN are believed to carry raw spectral signals from the sensory receptors (UV–, S–, M – & L– channels); as a result, they were not understood up through the early 1990's. The labels "Pγ?" and "PγPα?" in this figure should be ignored. The 100,000-150,000 number given by Cowey & Stoerig, is higher than found in other source material and is considerably higher than the number of photoreceptors (23,000) within the foveola of the human retina. Additional research is needed to resolve the precise character of all of the neurons in the optic nerve associated with the PGN-pulvinar pathway.

1.5.2.2.1 The cell and its environment

The cell and its environment can be described from a variety of perspectives. For the purposes of this work, the primary interest is on their electrical parameters. The fundamental, or minimalist, cell is a space surrounded by a plasma membrane and containing all of the constituents required to maintain the status of the cell. At the next level, the cell also contains certain constituents required for the cell to perform its role within the context of the whole anima. Both cells must interact with the surrounding environment. This environment must support a variety of chemical constituents and provide a set of electrical parameters compatible with the needs of all cells in the local area.

The plasma membrane of the fundamental cell is usually discussed as if it were uniform in its physical and chemical parameters. This is not generally the case at the most detailed level. The typical plasma membrane, as in all biological membranes, consists of two monomolecular lipid layers arranged with their hydrophobic terminals facing each other. Many of the membranes associated with a single cell are differentiated into separate functional regions. In some of those regions, the two bilayers are chemically symmetrical. This arrangement forms a nearly perfect electrical insulator. In other regions, the membranes are generally formed of a bilayer of two separate, lipid materials. This arrangement forms a nearly perfect electrical diode. To document these electrical properties requires a greater degree of experimental precision than found in most of the neurological literature to date.

It has long been known that the plasma, or cytosol, within a cell takes on a different electrical potential than that of the environment surrounding the cell. If the plasma membrane was a uniform insulator, this potential could be considered caused by a one-time event that introduced more negative charges into the space surrounded by the plasma membrane. However, when part of the plasma membrane forms an electrical diode, there is a need for a continuous process to maintain this electrical potential difference. There has been an ongoing effort to determine the mechanism that provides this potential difference. The neurological community has generally assumed that the mechanism involves an ion-pump that somehow transfers ions across the membrane to create this potential difference. The search for and definition of this pump has been fruitless to date. There is another mechanism on the periphery of the chemical field, electrostenolytics, that provides a simple solution to the requirement. Electrostenolytics is the field of electrical reactions occurring on the surface of a substrate, here the plasma membrane. Whereas the subject is usually looked upon as involving a reaction occurring entirely on one side of a substrate, this is not the total scope of the field. Electrostenolytics can employ a reaction on one surface of a substrate to cause a potential difference across the underlying substrate if that substrate exhibits the proper electrical parameters. For an asymmetrical plasma membrane coated with a set of appropriate reactants, the reaction will cause an electron to penetrate the membrane. This will result in a potential difference between the surfaces of the membrane. This potential will dissipate over time as a function of the capacitance and the resistive impedance of the diode formed by the membrane. However, a continuous reaction at the surface can sustain a significant potential indefinitely. This mechanism is the source of the potential in the typical biological cellular system. In support of this mechanism, the surrounding environment must maintain the necessary reactants while removing the reaction products. If the individual cells are to react with each other, in terms of electrical performance, an environment providing a degree of electrical conductivity commensurate with these local interactions is also necessary.

Because of the requirement for local electrical conductivity of the environment throughout the animal, there is also a finite conductivity between any two global points within the fluid environment of the animal. Investigators frequently take advantage of this fact to study processes at one location by using electrical probes at other locations. However, they do not always recognize that the local electrical environment may vary considerably within the animal. This variation can affect their measurements considerably and must be accounted for. It is particularly important in the electroretinogram (ERG).

1.5.2.2.2 The neurons

Describing neurons from a morphological perspective without understanding their electrophysiology is difficult. They are highly specialized cells with highly ramified “trees” associated with their “input” structures and simpler structures associated with their “output.” In the morphological context, the terms input and output are assigned based primarily on their position in the overall neural network. When the cells are described in terms of their electrical performance, it is an entirely different situation.

A better insight can be obtained by recognizing the neuron has the primary responsibility for passing an (electrical) signal from one point to another. To perform this function continuously, it must be supported by the necessary metabolic mechanisms. It must also be supported by the necessary electrical mechanisms, such as the electrostenolytic mechanisms mentioned above.

Based on this context, neurons can be looked at as specialized cells that can be divided into two major portions. One portion is an electrical pathway containing an active electrolytic device, similar to a transistor and known as an

Activa. Each Activa is a three-terminal electrolytic device. The input structures to such a device consist of two distinct electrolytic conduits, the dendrite and the podite. These conduits may be simple tubes extending from a contact point with another neuron to the site of the Activa. Alternately, they may be extremely ramified "trees" of tubes converging on the Activa from a very large number of individual connections, synapses, with other neurons. The output conduit, commonly labeled the axon, extends from the Activa to a connection region where it ramifies into many synapses, normally in a confined region, with subsequent neurons. The second portion of the neuron consists of the nucleus and other components required to support the metabolic growth and operation of the cell. The nature of the synapse is electrical in character. This fact will be introduced in **Section 1.5.2.2.3** and explored in detail in **PART D**.

> **It will be shown in this work that the neuron and the synapse are essentially electrolytic, and not chemical, in their operation. Although this assertion has been controversial for many decades, one can only understand the operation of the neural system by accepting this premise.**

With the acceptance of the electrolytic nature of the neuron and synapse, it becomes straightforward to describe the operation of the entire neural system at any level of detail desired. Such descriptions will occupy a major part of **PART C** (the details) and **PART D** (the operational aspects) of this work.

Each neuron contains multiple individual spaces (conduits, nuclei, etc.) within a common external envelope (plasma membrane). These spaces are generally enclosed by both exterior membrane (plasma membrane) and interior partitions (cyto-membranes). These membranes are generally highly resistive to the flow of electrical charges and virtually impervious to ionic flow on a short timescale basis. This allows each space to exist at a different electrical potential than adjacent spaces and the surrounding exterior fluid matrix. To document these potentials requires a greater degree of experimental precision than found in most of the neurological literature.

Many membranes associated with a single cell (neuron or not) are differentiated into separate functional regions. In those regions associated with electrical functions, the membranes are generally formed of a bilayer of two separate, lipid materials. This arrangement forms a nearly perfect electrical diode. In other regions, the two bilayers are chemically symmetrical. This arrangement forms a nearly perfect electrical insulator. To document these electrical properties requires a greater degree of experimental precision than found in most of the neurological literature.

Figure 1.5.2-6(A) presents a typical bipolar neuron, in the functional context of the retina although it has historically been labeled a monopolar neuron by the general morphologist. The functional portions of the bipolar neuron are the dendrite (acting as an input structure), the axon (acting as an output structure) and the active region labeled the conexus. The rest of the bipolar neuron performs only metabolic tasks required to keep the neuron functional. **(B)** shows the same bipolar neuron stripped to its functional essentials, the area within the conexus. The input signal current, the output signal current and the electrical bias enter and leave the neuron through specialized portions of the plasma membrane of the cell. These will be discussed in the next section. Within the cell, these currents travel in conduits normally described as reticulum by the morphologist. **(C)** shows the same elements as **(B)** using only electrolytic symbols. The heart of the conexus is seen to be an Activa, the electrolytic semiconductor device at the heart of every conexus. This device can be described as a conventional pnp type transistor made out of biological material rather than man-made material.

1.5.2.2.3 The fundamental synapse

Based on the above discussion of the cell, the environment and the neuron, seeing that the synapse between two neurons is actually the connection between two conduits is not difficult. It is the connection between an axon of one neuron and a dendrite or podite of a second neuron. Thus, the synapse is functionally identical to the conexus region of the neuron shown above. The other structures of the individual neurons, such as the nucleus, play no direct role. It will be developed in detail in **PART C** and **PART D** that the connection between these two conduits is formed by another active semiconductor device known as an Activa.

The synapse is most easily illustrated initially because it only involves two unique conduits arranged in a unique spatial configuration and immersed in a surrounding medium. **Figure 1.5.2-7(A)** illustrates the fundamental synapse between two neurons. The situation between two axon segments within a single cell (a Node of Ranvier) is not significantly different from this configuration. The figure attempts to illustrate both the morphologically and electrolytically significant elements of the junction. For convenience, it is divided into an upper and lower half although the actual situation frequently involves the electrolytic signal path being at the center of a symmetrical structure. The upper half illustrates the support functions near a synapse. The primary support function is that of providing electrical power to the neuron via electrostenolytics. The lower half illustrates the signaling path associated with a synapse of the neurological system. The primary role of this signaling path is the efficient transfer of an electrical current from the antidromic to the orthodromic conduits forming the synapse. The figure is not to scale. The upper half, which can be observed optically is immensely larger than the lower half. The lower half, also known as the synaptic cleft, can only be observed in detail with the electron microscope. The oval shape depicts a large vesicle pressing one membrane against the other. In actual synapses, this oval is usually replaced by an array of smaller vesicles similar in size to those shown elsewhere in the figure. The membranes shown are both bilayers of lipid material. The membrane material of the two cells generally appears in at least two specialized forms. The specialized membrane found in the region of electrostenolytic processing and near the synapse is that of an asymmetrical bilayer of lipid liquid crystals. This asymmetrical layer exhibits the electrical properties of a diode. Other areas of the membrane that play a lesser electrolytic role may be asymmetrical or symmetrical.

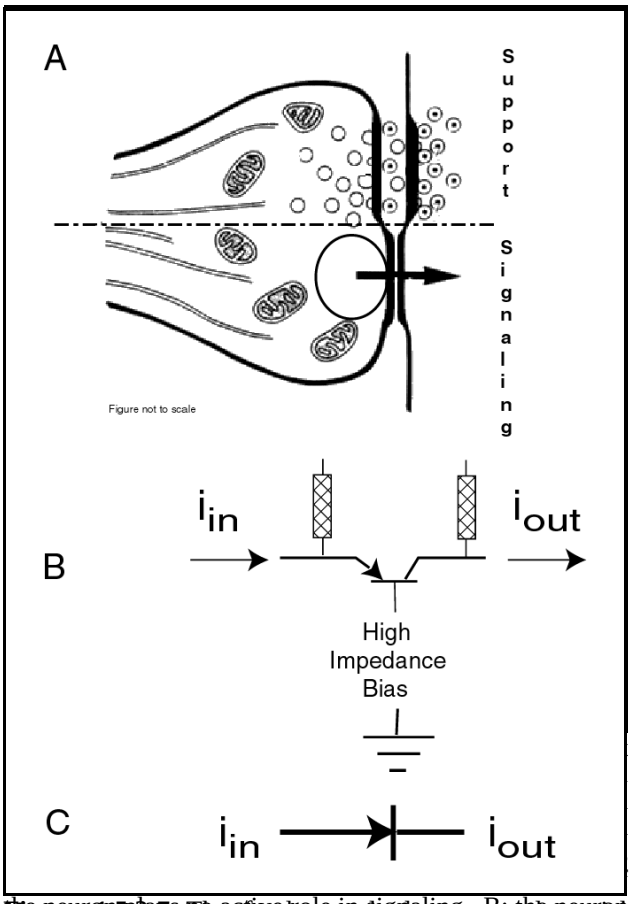

Figure 1.5.2-7 The fundamental elements and spatial relationships of the synapse. **(A)**; Figure is not to scale. The upper, support, region is immensely larger than the lower, signaling, region. The plasma membranes are each about 150 Angstrom thick. The two bilayers forming the plasma membranes of the two cells are specialized as a function of their position and function. While the overall synapse may have a diameter of several microns, the narrow region used for signaling, the synaptic disk, is less than one micron in diameter. The spacing between the membranes in this region is less than 100 Angstrom. The synaptic disk is not resolvable by simple light microscopy. **(B)**; The equivalent electrical circuit of the synapse. **(C)**; The simplified equivalent circuit frequently measured in the laboratory. See text.

The interstitial material in the upper half is readily identified by micro chemical analysis and is known to consist of elements of energy releasing metabolic cycles. The materials within the conduits are less well characterized.

Note the physical dimensions associated with the signaling path. Shepherd has quoted Gray regarding the diameter and spacing of these synaptic clefts. The spacing being on the order of 20-30 nm using the measuring techniques of the 1950s. The diameters are described as up to 1-2 microns for Type I junctions and less than 1 micron for Type II junctions. The spacing dimension is only resolvable with very high resolution electron microscopes. A more recent value of 100 Angstrom will be used for this spacing. The small amount of hydronium filling the space between the two membranes, especially in the situations discussed in the next paragraph, is frequently encountered as “ice”

during sample preparation by the electron-microscopist.

In more complex synaptic situations, two alternate physical configurations are found. In one, several separate signal paths connecting to different orthodromic neurons may be found in a very small area served by a single support structure. Alternately, a single signal path may require a higher current capacity than achievable within a single unit synapse. In that case, the overall device may consist of a group of individual devices within a local area defined as unit synapses in the next section.

(B) shows the equivalent electrical circuit for the synapse *in-vivo*. It shows the conexus consists of three primary elements; an Activa in the center plus two distinct electrical components (crosshatched) that represent both the electrostenolytic potential supply and the load impedance associated with that supply. For synapses, the contact between the base of the Activa and the surrounding fluid matrix is via a high impedance circuit that may include a bias potential source.

(C) shows the equivalent circuit as measured by a number of investigators *in-vivo* who were not aware of the more sophisticated nature of the actual conexus. The characteristics of this equivalent diode are well documented in the literature. The capacity of this diode depends on its physical dimensions. If a conexus is removed from an animal and washed thoroughly before evaluating, removing the electrostenolytic coatings is common. That action destroys the functionality of the conexus. The data collected subsequently does not represent the actual *in-vivo* circuit.

1.5.2.2.4 The unit synapse

When examined under very high magnification, the synapse is seen to be formed of an orderly array of smaller units. Each of these units makes up the minimum physical and electrical structure required to achieve transistor action and thereby move electrical signals across the junction with minimal loss. These units will be defined as unit synapses in this work. The term is to be differentiated from Shepherds terms simple and specialized synapses[155]. These terms refer to the complete synapse associated with the synaptic cleft. Use of the unit synapse nomenclature allows the total signal handling capability of an individual synapse to be described in terms of multiples of the capability of the unit synapse. The unit synapses are physically formed by vesicles found within the plasmas of the adjacent conduits. Shepherd has provided dimensions for these vesicles ranging from small (40-60 nm diam) to large (100-160 nm diam). The spacing of the vesicles ranges from very periodic to clustered. Based on these nominal values, the unit synapse will be defined as having an individual diameter is usually near 200 Angstrom[156] and a gap width of 100 Angstrom.

1.5.2.2.5 The photoreceptors, ganglion and other cells

In the upper left center of [**Figure 1.5.2-2**], four photoreceptor cells are shown. Each cell is divided into three parts, the soma, the IS and the OS. The OS's are further labeled L-, M-, S- & (UV) to show the spectral options available. Each IS is shown with an ellipsoid, the black dots, immediately behind the Optical focal surface. These elements collimate the light entering from the left and insure its efficient insertion into the OS elements. The somas are shown to the left of the Outer Limiting Membrane, OLM, to emphasize they are supplied metabolically from a different source than are the IS and OS elements. The somas are shown in the optical path. This is the norm in the reversed retina of the chordate eye, except in the part of the fovea where they are displaced to the side. The soma plays no significant role in the visual process.

The other types of neurons involved in vision are not shown explicitly in [**Figure 1.5.2-2**]. The details of these neural cells are too complex to be addressed in this introduction. They are all based on simple modifications of the fundamental electrolytic circuitry of the bipolar neuron shown in [**Figure 1.5.2-3**]. The circuitry of the photoreceptor cells, the amercine cells, the ganglion cells and the stellate cells will be developed in detail in **Chapters 12, 13, 14** and **15** respectively.

1.5.2.2.6 The vascular supply

The vascular supply to the eye divides in the region of the blind spot. One branch serves the neural and housekeeping functions of the retina distal to the OLM. The other branch serves the choroid and the retinal pigment epithelium (RPE). The drawing attempts to illustrate the limited capacity of the small arteries and veins, particularly serving the soma and the portion of the IS supplied from the distal side of the OLM. The length of the path $\varepsilon-\chi$ is

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[155]Shepherd, G. (1988) Neurobiology, 2nd ed. NY: Oxford Press pp 77-83

[156]Raviola, E. & Gilula, N. (1975) Intramembrane organization of specialized contacts in the outer plexiform layer of the retina. *J. Cell Biol*. vol. 65, pp 192-222

relatively long. There is a time constant associated with the flow of nutrients from the manifolds to the individual photoreceptors that must be considered when making measurements of the transient performance of the eye to illumination. The length of the path $\alpha-\beta$ between the vascular manifold of the head and the limited capacity manifold within the eye must also be recognized. This path also exhibits a time constant that must be considered. The ellipse immediately to the right of the Ocular Platform is included to emphasize the length of the path $\alpha-\beta$. It also emphasizes the fact that the structure called the optic nerve includes auxiliary functions, both the blood supply and the nerves controlling the muscles of the lens and iris.

1.5.2.2.7 The muscles and optical mechanisms supporting vision

The muscles are shown as small open circles connected between the various elements and platforms in the lower left of [**Figure 1.5.2-2**]. They control the relative motion between the different platforms and the condition of the elements in the light path shown in the upper left. A and B are drawn to show two separate eyelids. A is normally opaque and acts as a shutter. B is frequently transparent and may also act as a nictating lens in semiaquatic animals. C is the iris and D is the conventional lens. The cornea is not shown. It may also be under muscular control to a certain degree (in a manner similar to the lens). The small 2 near the actuator (muscle) controlling the Ocular platform indicates the number of degrees of freedom of motion. Because of the musculature of the Ocular platform, there is also a small third motion of the Ocular consisting of rotation about the line of sight. The 6 next to the skeletal actuator indicates the complete freedom of the animal to move in any direction.

The fact that the muscles of the oculomotor system exhibit a dual capability reflected in their anatomy is not illustrated in the figure. These muscles are believed to be unique in that they exhibit both a coarse but large and relatively slow contraction capability and also a very fine, fast contraction capability over a restricted range. These features are developed in detail in **Section 7.3**.

1.5.2.2.8 The signal processing matrices

The signals emanating from the photoreceptors are shown dividing and passing through two processing matrixes in parallel. Subsequently, the brightness signals are shown being passed to both the brain and a second lateral processing matrix. The brightness processing matrix is primarily involved in summing the spectral signals prior to their delivery to the magnocellular section of the brain. The first lateral processing matrix is primarily involved in performing subtractions between the different spectral channels in order to form the chrominance signals for delivery to the parvocellular section of the brain. There may be two or three signal channels emanating from the lateral processing matrix as indicated by the symbol containing "n." This matrix is generally associated with the "horizontal cells." The nuclei of these cells are located at the distal extreme of the inner nuclear layer.

The signals from both the brightness and first lateral processing matrixes are shown dividing on the way to the brain. Besides the well documented and reported division of the LGN into two portions, each receiving a different set of signals, there is a third part of the brain that receives signals directly from the eyes. The information from the foveal receptors is passed directly to the Pretectum. **Chapter 15** will document how signals received in the magnocellular and parvocellular portions of the LGN are processed for a variety of purposes. These two sections of the brain eventually cause commands to be generated within the Superior Colliculus, part of the motor control portion of the brain. These commands are also sent to both the Pretectum, for further processing and action, and back to the memory section of the brain. One of their uses in the brain is to "blank" the short term memory during saccades of the eye. The foveal signals pass from the retina directly into the Pretectum. This is probably to reduce the time delay compared with those signals being delivered to the LGN. The lower time delay is important in the generation of precision scanning signals related to the scanning of imagery in fine detail by the foveal portion of the visual system. It is not clear whether signals from the first lateral processing matrix are delivered directly to the Pretectum or not.

The second lateral processing matrix is believed to be more important in some chordates, other than humans. It is responsible for preparing geometric indicator signals for transmission to the brain. Many psychophysical experiments on members of the cat family show they may perform a significant amount of signal processing aimed at determining the shape and direction of movement of objects in their visual field. Such processing in humans is thought to be less developed. However, it is likely that such processing is used in determining the motion vector of projectiles approaching the human, from a rock to a baseball. Little can be said definitively concerning this second level of signal processing, nominally associated with the amercine cells at the edge of the inner nuclear layer next to the inner plexiform layer. Assuming that this matrix accepts processed brightness information to achieve maximum sensitivity under low light conditions would be logical. It is not clear whether the output of this matrix is passed to both the LGN and the Pretectum or not.

1.5.2.2.9 The signal transmission system

The signal transmission system, consisting of the ganglion cells, their projection through the optic nerve, and the decoding cells in the brain receiving the signals from the ganglion cells are not shown in this top level schematic. This is because they are designed to be transparent to the overall operation of the visual system. They do play a significant role in flicker phenomena as will be seen in **Chapter 17.**

It is unfortunate, but absolutely necessary, that portions of this model do not build on models developed from the 1930-50's forward because of some basic decisions made by the vision research community. This was a time when;

+ mathematical rigor in the vision research community was not maintained and sometimes frowned upon.

+ inadequate attention was given to the technology and scientific understanding available in parallel fields of science, specifically the rules and technology of dye chemistry.

+ Many modern tools of quantitative analysis were not yet available. A specific example being nuclear magnetic resonance techniques for determining the structure of a given chemical compound in detail.

1.5.2.3 Important cornerstones

1.5.2.3.1 Photo-excitation

Chapter 12 and **Appendix A** presents a complete description of the process of photosensing employed in biological vision. The process is quantum-mechanical in nature but it does not involve any steric changes in the constituents. That discussion will end with the presentation of the complete Photoexcitation/De-excitation equation (the P/D equation) of vision. The P/D equation describes the actual process in unparalleled detail, with unequaled mathematical rigor and unrivaled experimental support. This will make the model and the P/D equation available to the entire visual science community for evaluation at the earliest feasible time.

It will be shown (recognized) that the P/D equation applies equally to all animals of the Phylogenic Tree. Application of the model to both "photoreceptor cells" of *Chordata* and the photoreceptor cells of "rhabdoms" is primarily a matter of size, geometry, temperature and sometimes choice of chromophore.

1.5.2.3.2 Impedance of biological tissue

There is an important axiom and corollary to the proposition that biological tissue has an impedance represented mathematically by a diode.

If the basic signal generated in vision is a charge of electricity (an electron = q), the rate of signal generation is given by a current, $i = dq/dt$. At any point in the circuit, the sum of the currents due to two different sources is added algebraically

> **+ currents representing the addition of signal currents in the retina represent the addition of the underlying signal currents.**

At any point in the circuit, the voltage related to this signal current is given by $V = Z(i) * i = K*\ln i$ and not $K*i$. This results in the following;

+ the sum of two voltages in the retina results in a voltage corresponding to the sum of two signal currents in accordance with $V_C = K_A*\ln A + K_B* \ln B$. V_C can be written as $V_C = K_C* \ln C$,

+ taking the antilog of the above equation results in a signal that is equal to the ***product*** of the two original signal currents, $C = (KA*KB*/KC) * (A*B)$,

+ where the asterisk is used to show multiplication.

therefore, the corollary is that:

> **+ voltage signals representing the addition of voltages in the retina represent the summation of the logarithms of the underlying currents.**

Thus, care must be taken to:

+ distinguish between the voltage at a node and the currents at a node.

+ determine what form of the signal is being used by the subsequent signal processing stage.

1.5.2.3.3 The Biological transistor

There is *overwhelming* evidence that the neuron incorporates a biological equivalent of the semiconductor transistor. The foundation for this proposition will be addressed fully in the **Appendices** of this work. One of the simplest applications of this biological transistor is to produce a voltage output that is proportional to the natural logarithm of the input current. Using this proposition and this simple application, elimination of all of the variable resistors found in so many piecemeal (floating) models used in vision research is possible. If the morphologists of the 1950's had been aware of Chapter 13 of the book Applied Electronics by Gray[157], they could have saved themselves a great deal of work. It shows how the simplest of transistors can perform the four major functions of the neural system. These are the pulse regenerating functions of a Node of Ranvier, the analog amplification functions of neuron cells such as the bipolar cells, the translation of analog signals into pulse signals in the ganglion cells and the subsequent recovery of the analog signals by the stellate cells. The Nodes of Ranvier are in fact biological transistors and provide a convenient demonstration of the physical properties and operating characteristics of the biological transistor. The synapse between neurons will also be shown to be formed by a biological transistor. Through this unique physical and electrical configuration, the electrical characteristics of the presynaptic and post synapstic cell walls are modified to overcome the objection stated by many[158] concerning the impedance level of those walls.

> Sir Barnard Katz stated a criteria very succinctly, although in the negative: "The presence of closed terminal membranes and extracellular spaces between two cells could not fail to impede the propagation of the nerve message by the ordinary electric process if the membranes have the same insulating qualities and the material of the external spaces has the same conducting properties at the synapses as elsewhere." The biological transistor is the very device that overcomes this criteria so naturally. The mechanism is called "transistor action." It is the same mechanism that separates two man-made diodes wired back to back from two man-made diodes on a common substrate called a transistor.

1.5.2.3.4 The thermodynamic environment

When discussing the application of the First Law of Thermodynamics in neural systems, it is necessary to consider the heats of formation of the various chemicals used to generate electrical power in the neural system. It is difficult to determine the energy consumed by the neural system without considering the products associated with respiration, ingestion and excretion.

The neural system in animals is to-date, unique among known communications systems. By omitting real resistors from most its signaling circuits and employing chemically reversible sources of electrical energy, the neural system avoids a principal limitation of man-made systems. To the first order, the neural system does not generate significant heat related to the signaling task. Failing to generate heat, the system does not employ a Carnot Cycle. Since it does not employ a Carnot Cycle, the system is not subject to the Second Law of Thermodynamics. As Schulman wrote in discussing the Second Law[159], "But–and this is the crucial thing–there are other situations where the law has no jurisdiction."

In place of the resistor, the neural system employs perfect electrical diodes, normally in shunt with the electrostenolytic power sources and capacitors, and active electrolytic semiconductor devices called Activas, that are biological transistors. Both the Activas and the diodes exhibit electrical characteristics that are basically those of a diode. However, and obviously, the Activa exhibits more complex characteristics than a simple diode. The result of the presence of these circuit elements is that nearly all trans-impedances measured in neural systems will appear nonlinear. They are frequently labeled "rectifying" in the recent biological literature. Such a brief label does not do justice to the neural system. Except in the case of the stellate cells, the diodes are not used as rectifiers. The description of a diode as a rectifier is usually employed where the applied voltage level is much higher than the threshold voltage of the diode (or diode-like) circuit. For lower applied voltages, and at various bias conditions for the Activa, the non-linearity of the diode is merely used to select an appropriate small signal impedance level from its overall impedance characteristic.

For oscillatory circuits, such as those used to generate and transmit action potentials, the Activas are used in large signal applications. However, there is virtually no recognition in the literature of how these circuits operate and few authors have used the term rectifier in discussing the action potentials.

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[157]Gray, T. (1954) Applied Electronics NY: John Wiley & Sons & London: Chapman & Hall pg.788-825
[158]Katz, Sir B. (1966) Nerve, muscle and synapse. NY: McGraw-Hill pg. 99
[159]Schulman, L. (2002) The Universe Next Door, –:Marcus Chown

1.5.2.3.5 The electrophysiological environment

The size of the major circuits of the neural system are not convenient for measurement by man. They are so small and compactly arranged, and so specialized that contacting them electrically in a straightforward way is difficult for man. Furthermore, their predominant nonlinear characteristics have made it difficult for man to relate to them conceptually. Nonlinear signal transmitting circuits, other than oscillators, were rarely used until the arrival of the semiconductor microcircuit.

The problem of size and access have been particularly difficult in understanding the operation of a projection neuron, and particularly the axon of such a neuron. This apparent circuit element (which is frequently a series of individual circuits at the cellular level) has been found to be linear, to be rectifying and to be saltatory at different times in the development of electrophysiology. The axon is certainly not linear from an electrical perspective. In fact, it is nonlinear in almost every known manner when it is examined at the subcellular level, e. g., the cell wall has differentiated dramatically into individualized areas that provide unique functions.

The individual active circuits of the neural system exhibit all of the unique electrical characteristics of equivalent man-made transistors. These characteristics account for many inconsistent and/or unreproducible electrical data points found in the literature.

The neurons and other cells of the neural system have been arranged in a very complex manner in relation to their environment. It is the electrophysiological requirements placed on the system that account for the many barriers between cell groups, found particularly in the retina. Without appreciating the purpose of these membranes, it is difficult to understand the operation of the retina in detail. The use of the electroretinograph (ERG) is entirely dependent on the presence and extent of these membranes.

The details of the electrophysiology of the neuron will be explored extensively beginning with **Chapter 10**.

1.5.3 This Presentation

To encompass the scope of material about the process of vision in animals, dividing the subject matter into several major subdivisions has been necessary. After this Chapter, which is envisioned as a global introduction, the work consists of five major parts and a series of appendices. The appendices were found necessary because of the overlap between technologies in some areas. These overlaps were so profound that it made it difficult to maintain the focus of a given discussion in the main part of the work. Therefore, occasionally, the discussion in the main text was truncated to maintain a given theme and reference was made to a more global presentation in the Appendices. This allowed the main presentation to be divided into five main areas;

PART A. The environment, contexts and phylogeny of vision
PART B. The photochemical aspects of the vision process
PART C. The electrochemical and neural aspects of vision
PART D. The signal paths, calculus, and psychophysics of vision
PART E. The Performance Descriptors of Vision
The Appendices
The Glossary, Bibliography and Index

Whereas **PARTS A, B & D** were expected to be the heart of the work, **PART C** fills a very large gap in the current literature of the visual process. Without this section, relating the experimental data related to the photometry and the electrophysiology of the eye directly to the action spectra of the eye is essentially impossible. **Part D** develops the detailed relationships of vision based on the three earlier parts. **PART E** was added to summarize the performance descriptors of vision, interpret certain clinical results in terms of the Theory and to address some remaining questions in the conventional wisdom. Providing new descriptors is more appropriate than attempting to defend old versions, even those enjoying international accreditation. This is because of the inadequate theoretical foundation of the old descriptors. However, traceability is provided.

Over the years, due to the lack of an adequate model, many “effects” have been noted concerning vision. These effects have frequently been described using the name of the discoverer. A section of **PART E** is devoted to placing these effects in the proper context of the overall vision model; showing how they arise and what parameters influence them. In several cases, this allows a restating of the effect in more precise terms. In a few cases, it allows the further expansion of a concept to explain or predict additional special effects.

PART E concludes with a brief discussion of several disparate areas. A short discussion is included concerning new and redefined research paths that have appeared based on this model. It suggests some possibly new paths of inquiry. It also highlights several experiments that could be used to provide significant confirmation of the theory

presented here.

As indicated above, the Appendices includes several focused studies that support the main work but are too detailed to fit easily into the main text. These include;

+ The complete solution to the Photoexcitation/De-excitation Equation
  A key part of this work for it leads to the basic understanding of the photodetection process.
+ The development of the Biological amplifier found in the Neuron
  A second key part of this work for it explains how the neural system can amplify and provide computational processing in the retina very efficiently.
+ An interpretation of the data base related to the Squid neuron
  Providing a broader and more comprehensive theory of the operation of the total neuron than can be obtained from the previous detailed studies of the axon alone.
+ Some material related to the extraction and characterization of the Rhodonine chromophores

+ The description of the reversible thermodynamics employed in the neural system
  An explanation of the unique method of energy usage/conservation used in the animal neural system

+ The presentation of the code used in neural signaling
  Specifically focused on describing the parameters involved in signaling to provide a rationale and foundation for most of the data in the literature
+ Tabular material relating to the spectral characteristics of the chromophores of vision

+ The Visual Signal Path in *Limulus*
  A comprehensive review of the complete visual system of a simple animal designed to integrate and rationalize the extensive studies carried out in the past using a variety of floating models and varying levels of technological sophistication.

Before proceeding to the body of this presentation, summarizing is advisable. The following subsections will provide both a summary of the overall Proposition embodied by this work and many Axioms and Corollaries that evolve from that Proposition. These summaries will be brief. The subject matter will be presented in detail in later sections.

1.5.3.1 The Fundamental Propositions

1.5.3.1.1 The Fundamental Proposition (of vision)

The Fundamental Proposition of this presentation is; **The process of vision in animals has sprung from a common ancestor, is based on electrolytic principles and is tetrachromatic when fully elaborated in a species.**

Expanding on this proposition,

+ All fundamental processes are the same throughout the animal kingdom; however, differentiation and adaptation have resulted in an immense morphological variety of visual systems.
+ The neurological elements of the visual process are based on electrolytic electronic principals and include an active biological device called an Activa™.
+ The photodetection process involves a homologous family of four chromophoric molecules which do not contain a protein ligand but must be present in the liquid crystalline state.
+ The generic eye in animals is tetrachromatic.
+ The retina of the human eye is tetrachromatic; however, the transmission properties of the lens and cornea exclude sensing of irradiation in the ultraviolet range.
+ The semiconductor based signal processing employed to transmit information from the photoreceptors to the initial cortical cells is sophisticated but conventional when related to man-made semiconductor circuits.
+ The power management system used in biological vision is unique and not used in man-made devices.

All of the psychophysical and behavioral aspects of vision can be explained with mathematical precision using the Fundamental Proposition. This statement can only be justified by providing the details of how biological vision operates in a comprehensive assortment of individual cases. This has been done. To aid the understanding of these cases, it is important that an additional level of information be provided to relate these cases to the Fundamental Proposition. This will be done through a series of Axioms and their Corollaries presented in the next subsection.

1.5.3.1.2 The Fundamental Proposition (of the photodetection system)

The photochemical foundation of the visual process predicts four chromophores for the generic visual system. While some animals may not employ all four, the great preponderance of animals do. While this statement may appear too strong, even Goldsmith has transitioned to this position[160]. Loew concurred with and paraphrased his views in 1994[161] saying "the relevant question is not why some species have UV pigments, but why some don't! Goldsmith actually said" Trichromacy is not the norm."

This position has been expressed most poignantly recently with the recognition that the human retina is tetrachromatic (See **Section 17.2.2**). It is the physiological lens of the human eye that restricts its performance to a trichromatic regime.

1.5.3.1.3 The Fundamental Proposition (of the neural system)

Because of its independent importance, a separate Fundamental Proposition (of the Neural System) will be presented in **Section 10.8.1** following the introduction of a detailed background in **Chapters 8** & **9**. It can be stated briefly as:

A restated Neuron Doctrine –The neuron is the fundamental biologically sustainable unit of the nervous system. It is the minimum viable cellular structure. Each neuron contains one or more fundamental functional (signaling) units internally and one or more external fundamental units connecting it to an orthodromic structure. Each fundamental functional unit consists of an active electrolytic semiconductor device, an Activa, supported by its peripheral electrolytic components.

> The following corrolaries apply to all neurons of the biological nervous system. They describe the fundamentally **analog** operation of all signal processing neurons. These are found in the retina, the central nervous system and at nodes and terminals of the peripheral nervous system.
>
> Every neuron contains at least one active electrolytic semiconducting device capable of amplification. (See **Section 10.3.4.3** for a definition of the term amplification.) The Node of Ranvier and the synapse are morphological labels for active electrolytic circuits containing at least one semiconducting device.
>
> If supported by electrolytic components of appropriate value, the **analog Activa within a neuron can be made to oscillate and generate phasic waveforms** (known as action potentials). Such circuits are used in the signal projection neurons of the nervous system. These are found in the optic nerve, the long neurons of the peripheral nervous system and in the commissure of the brain.
>
> The vast majority of the neurons of any neural system (over 94% in humans) operate in the analog mode (process electrotonic signals).
>
> Although employing internal negative feedback widely, external negative feedback is not used in the neural system except in control loops involving muscles.

1.5.3.2 Other Axioms & Corollaries based on the Propositions

The following material may be provocative but it is not designed to be argumentative. Only the text has the space to provide the entire justification for the axioms and corollaries presented here. It is supported by many references. You are welcome to explore that text, with its supporting graphics at your leisure. The Axioms will be divided into seven categories:

1. Overall principles
2. Detection photochemistry
3. Neurons--classification & function
4. The Activa--the biological transistor in the neuron

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[160]Goldsmith, T. (1990) Optimization, constrain and history in the evolution of eyes. *Quart. Rev. Biol*. Vol. 65, pp 281-322

[161]Loew, E. (1994) A third, ultraviolet-sensitive, visual pigment in the Tokay Gecko (Gekko gekko). *Vision Res*. vol. 34, no. 11, pp 1427-1431

5. Signal processing in all domains
6. Signal encoding
7. Psychophysical effects

Most Axioms will be followed by numbered Corollaries associated with it.

1. Overall principles

Vision is fundamentally a tetrachromatic process in animals
#1 Most aquatic animals are sensitive to four (4) discrete spectral regions during at least part of their lives.
#2 Aphakic humans exhibit a luminosity spectrum with a relative peak near 342 nm.

The Vision Process is fundamentally the same in all animals

Biological vision involves two fundamentally different optical configurations.
#1 Animals living in water employ a "simple" optical system
#2 Animals living in air employ an immersed optical system
#3 The cornea is the principle optical element in animals living in air
#4 Animals frequently traversing the air/water boundary have dually or switchable optical systems

Vision involves detecting a temporal or spatial change within the field of view
#1 The animal eye does not form an image and is blind without change in the field of view
#2 The minimal change required to image a scene is provided by the tremor of the ocular muscles

Vision is based on reversible thermodynamic principles
#1 Living tissue is not a closed system and the Second Law of Thermodynamics does not apply
#2 Vision expends essentially no energy in the form of heat

Vision is based on the electrolytic semiconductor, as opposed to the solid state semiconductor

The dynamic and transient processes in vision have not received appropriate attention in the literature

The luminance adaptation curve is a record of transient processes
#1 The fundamental luminance adaptation curve only involves one type of photoreceptor cell
#2 The complete luminance adaptation curve includes both on and off transients
#3 The off-transient of the luminance adaptation curve is caused by two or more processes in series
#4 The transients are associated with the ability of the power supply to service the active devices in the signal processing path

The formation and phagocytosis of disks in the Outer Segment (OS) is a dynamic process
#1 The disks are formed by secretion followed by extrusion, as opposed to invagination
#2 The disks in humans at 37 Celsius have a life expectancy of 170 hours (7 days)

2. Detection photochemistry

No achromatic, or broad spectral band photoreceptors are required to explain the process of vision in animals
#1 All of the chromophores of vision in any animal can be described as sensitive to the ultraviolet wavelength, short wavelength, medium wavelength or long wavelength
#2 The wavelength of peak sensitivity of these chromophores at 37 Celsius are 342, 437, 532, & 625 nm. respectively, +/- 2 nm.
#2 All photoreceptor cells in a given animal can be separated into groups containing one of these four chromophores of vision

Photodetection uses one or more of the homologs of Rhodonine as the chromophore

#1 Phototransduction involves chromophores existing in the liquid crystalline state
#2 The chromophores are resonant conjugated hydrocarbons of the retinoid family
#3 The chromophoric molecules do not contain any protein as a ligand
#4 The chromophores are normally deposited on a protein substrate for morphological and optical reasons

3. Neurons--function & classification

All photoreceptor cells are neuro-secretory cells of the exocrine type

#1 The Outer Segment (or rhabdomere) are external to the photoreceptor cell wall
#2 The substrate of the disks (or rods of rhabdom) are a protein extruded by the photoreceptor cells
#3 The disks in a given OS are coated by a liquid crystalline mono-layer of one of four chromophores
#4 The chromophoric material is produced in the Retinal Pigment Epithelium (RPE)
#5 The chromophoric material is transported to the OS through the Inter-Photoreceptor Matrix (IPM)
#6 The chromophore adheres to the substrate by hydrogen bonding (also known as Van der Wall forces)

All neurons involved in vison incorporate at least one active electrolytic semiconductor device
#1 The active device is not directly associated with the Soma
#2 The active device is defined at the junction of the dendritic and the axonal structures of a given cell

The dominant mode of signal transmission in vision is between an axonal structure of one cell and the dendritic structure of a second cell
#1 The junction of one axonal structure and a more proximal dendritic structure forms an active device, colloquially known as a “gap junction”

Both the active device within a neuron and the active device between two neurons are called Activa
#1 The Activa is an active electrolytic semiconductor device
#2 The Activa is a direct analog of the man-made solid state semiconductor device called a Transistor
#3 The Activa is a three terminal device
#4 There may be multiple connections to any terminal of an Activa

Neural signal transmission involves devices and circuit elements existing in a combination of the electrolytic and the liquid crystalline state
#1 There are no metallic conductors in the neurological system of vision
#2 Charge transmission in liquid crystals does not involve the motion of atomic nuclei or of free electrons
#3 "Hole" transport is the dominant mechanism of charge transport between definable elements in vision
#4 The predominant signal delay in electrolytic devices is due to the limited mobility of the dominant charge carrier in electrolytic circuits
#5 Latency, as an effect, is primarily a delay in the expected response to a transient signal input due to the limited mobility of the dominant charge carrier in the material forming the electrolytic circuit

As in man-made transistors, Activa can be categorized with respect to their parameters
#1 These parameters are tabulated in the main work for 6-8 types of Activa

4. The Activa--the biological transistor in the neuron

All known Activas are of the pnp type
#1 The device consists of two materials in which the majority carrier is of positive polarity
#2 The two materials are separated by a third material in which the majority carrier is of negative polarity
#3 The space between the two p-type materials is typically less than 100 Angstrom

Activas are normally biased electrically like transistors of the pnp type
#1 The output terminal, known as the collector or the axon is normally biased with respect to the third terminal to inhibit current flowing in the axon lead of the device (a negative bias)
#2 The input terminal, known as the emitter or the dendrite, is normally biased with respect to the third terminal to inject current into the device (a positive bias)
#3 The third terminal, known as the base or the poda, is normally the reference terminal of the device

Activa can provide a variety of signal manipulations
#1 When biased as above, the injection of a current at the dendrite will result in the flow of an equal current in the axon of the device (the voltage at the axon will track the voltage at the dendrite without inversion)
#2 When biased as above, the injection of a current at the poda will result in the flow of a much larger current of opposite direction at the axon of the device (the voltage at the axon will move in the opposite direction to the voltage at the poda and the change will be much larger)
#3 The Activa exhibits intrinsic (internal) positive feedback that can lead to continuous or intermittent oscillations, known as “Action Potentials.”
#4 The time duration between intermittent oscillations is easily controlled by the current injected at the dendrite terminal.
#5 The duration of the individual pulse during oscillation is controlled by the capacitance associated with either the

dendritic or axonal lead relative to the poda
#6 An Activa on the threshold of intermittent oscillation may begin continuous oscillation upon the addition of a capacitance related to an electrical test probe

5. Signal processing in all domains

All photoreceptor cells exhibit a more negative voltage, a hyperpolarization relative to the quiescent voltage, at their axon upon the illumination of their chromophore
#1 All photoreceptors use an internal differential amplifier consisting of two Activas
#2 The current through the collector of the input Activa increases with illumination
#3 Illumination causes a decrease in the voltage, a depolarization, at the collector of the input Activa which is measured as a decrease in the voltage of the Inter Retinal Matrix surrounding the outer portion of the photoreceptor cell
#4 The current through the output Activa is reduced with increased illumination
#5 The reduced current through the collector of the output Activa results in a hyperpolarization, an increase in the negative quiescent voltage at the pedicle of the cell.
#6 The above two currents sum to a constant value in the common emitter circuit of the differential amplifier

Vision is based on an exponential impedance
#1 The resistive component of each circuit element in vision is nonlinear
#2 Ohm's Law does not apply to the vision system
#3 Kirchoff's Laws are appropriate for describing the visual system.

Vision employs non-dissipative thermodynamic principals
#1 The fundamental impedance is non-dissipative
#2 The fundamental power source is reversible

Vision is based on exponential arithmetic
#1 The luminosity function is given by the summation of the logarithms of the amplitude of the current in each chromophoric channel at a given luminance level.
#2 The CIE Luminosity Function is a small signal approximation to the actual luminosity function
#3 The CIE Chromaticity Diagram is a small signal approximation to the actual chromaticity diagram

The primary method of signal processing in vision is positive and negative summation
#1 Summation is an inherently symmetrical process
#2 Inhibition is an inherently asymmetrical process and is not used in vision

Feedback has not been adequately studied regarding its use in vision
#1 External feedback does not play a general role in vision
#2 Internal feedback plays a dominant and very important role in vision
#3 External feedback is used in the Precision Optical System to control the oculomotor muscles

6. Signal encoding

Signal encoding is used in the higher animals to transmit information to the brain efficiently
#1 "Action Potentials" are a representation of signal encoding
#2 Signal encoding is not required for transmission of signals over short distances

Signal encoding in vision is by time-interval modulation
#1 Ganglion cells are used in two different circuit configurations for signal encoding
#2 Decoding of time-interval modulated signals is performed in the brain by stellate cells

7. Psychophysical effects

State of the art experimental accuracy requires close environmental control
#1 the temperature should be controlled to +/-0.1 C.
#2 the temperature should be measured to +/-0.1 C.

Precision spectral measurements require high accuracy
#1 Wavelengths should be measured to +/-2 nm accuracy
#2 Spectral filters should not exceed +/-5 nm in half-amplitude width

Luminances (radiances) must be controlled to +/-10% in precision measurements
#1 The sensitivity of the visual process is a continuous function of the luminance
#2 The temporal frequency response of the visual process is a continuous function of the luminance
#3 The spectral sensitivity of the visual process in higher animals varies with luminance and it can be related to four distinct luminance regions
#4 There are no adequately defined photopic, scotopic, mesotopic or hypertopic levels in the literature

General laboratory photometers cannot be used in precision measurements
#1 General laboratory photometers are not calibrated against real luminosity functions
#2 Compensations of general laboratory photometers for photopic or scotopic conditions are inadequate

Conventional Ringer solutions are not adequate for Vision research
#1 Washing neurological material in water or Ringer solutions removes important electrolytic material
#2 Ringer solutions do not contain the metabolic materials needed to sustain neurological activity

Dim red light cannot be used in accurate spectral experiments involving vision
#1 The L-channel chromophore has significant sensitivity to dim red light (including a Safelight)
#2 Use of a dim red light anytime disturbs the adaptation conditions of the specimen
#3 Most laboratories have not studied the conditions under which a Safelight can be used in photography

1.6 New Descriptors of vision based on this work

With the significantly more detailed model of the visual system available from this work, it becomes possible to provide more comprehensive, and accurate, descriptors of the visual process. These new descriptors are both mathematical and graphic in style. They are addressed in detail in **Chapter 17.**

The most fundamental change in the baseline of vision is recognition of the fact that biological vision is tetrachromatic. All phyla of animals employ four different chromophores to sense light in the ultraviolet, short, medium and long wavelength regions of the visual spectrum. It is only in humans, and other large chordates that vision in the ultraviolet region is lost due to absorption of the ultraviolet light due to the thickness of the lens of the eye. Small chordates have demonstrated ability to sense ultraviolet light in the 300–400 nm region. These capabilities will be explored extensively in subsequent chapters. Humans are left to wonder what other animals see in the ultraviolet region of the visual spectrum.

1.6.1 The fundamental equations of vision

No fundamental equation for the overall process of vision has appeared in the literature, although such an equation has appeared for the more limited regime of trichromatic color vision. Such fundamental equations are needed to define the fundamental architecture of the system and aid researchers at more detailed levels. The overall process of vision has been defined conceptually as linear for a very long time. The conventional Color Equation is based on this concept, as are many other hypotheses involving additivity and superposition. Adopting the concept of linearity has been a fatal error in any analyses of the visual process. **Figure 1.6.1-1** provides a synopsis of the nonlinear and asymmetric processes occurring in the visual processes of animals. The transfer function of the adaptation amplifier found in the photoreceptor cells of all animals is a stunning example of how far from linearity the visual system diverges. This amplifier has a transfer function that is exponential with an argument that can vary from three to six dynamically as a function of the stimulus. The visual process in animals is **not** linear in any sense. Any hypothesis based on the assumption of linearity is bound to fail.

The most fundamental non-linearity in the process of vision is at the output nodes of the distribution amplifiers, shown by circles. At this point, the current originally generated in proportion to the illumination creates a voltage by passing through a diode. The result is a voltage that is the logarithm of the current. This voltage is sensed by the processing amplifiers that follow. By taking the logarithm at this point and summing them, the individual absorption characteristics of individual photodetection channels are merged into a single overall absorption characteristic.

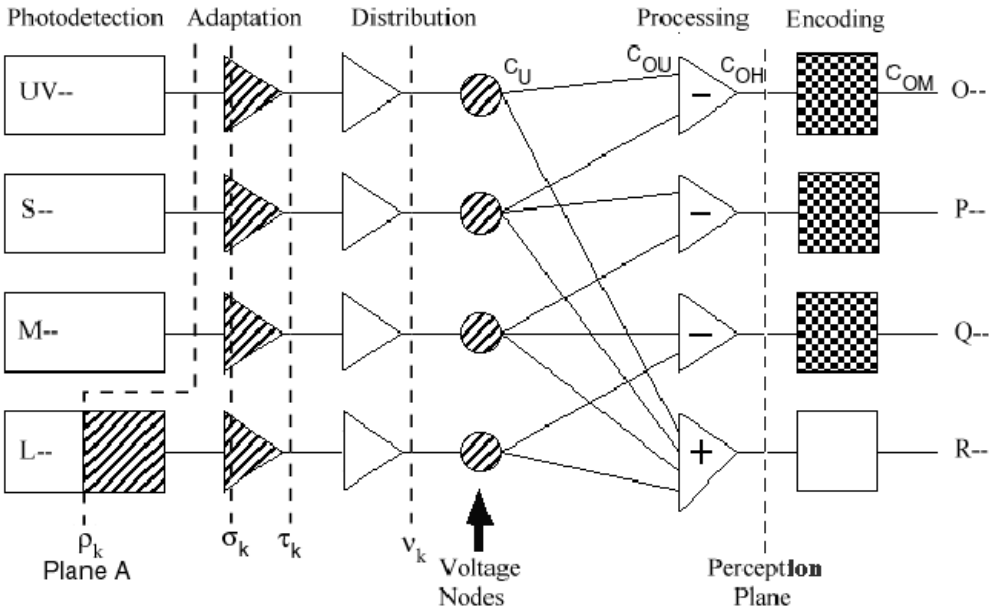

Figure 1.6.1-1 Principle areas of non-linear and asymmetric signal processing in the retina. Areas of non-linearity are shown cross-hatched. Areas of asymmetry are shown checkered.

Figure 1.6.1-2 from Saszik & Bilotta[162] provides very good support for the exponential nature of the photodetection process in vision. Although the figure describes the photodetection process via an ERG acquired under transient conditions, it is clearly indicative of the overall exponential characteristic of photodetection. The right-hand scale has been added to this figure for discussion purposes. This scale would show the stimulus level applied to the zebrafish if it were logarithmically related to the measured response shown in microvolts. The similarity between the auxiliary scale and the values shown within the figure speaks for itself.

Lacking a fundamental mathematical equation of vision, the community has adopted the fundamental laws of pigment mixing in object space to explain the physiological sensing of color in perceptual space. However, the perception of the human visual system has been known to differ from that of photometric instrumentation employing linear signal manipulation for a long time.

An argument can be presented that the visual process is linear for small signals. However, the signal manipulations found in the retina forcefully refute this claim, especially for the color aspects of vision.

An equally important feature of the vision process involves the independent manipulation of the brightness and the chrominance information beyond the distribution amplifier output nodes. This independence allows the separate mathematical description of each signal channel.

> In the following equations, the constants K have been written with a single subscript for simplicity. In use, they should be written with a second subscript indicating the channel they apply to, O, P, Q or R. The derivation of all of the equations in this section is presented in detail on **Chapter 16**.

[162]Saszik, S. & Bilotta, J. (1999) The effects of temperature on the dark-adapted spectral sensitivity function of the adult zebrafish. Vision Res. vol. 39, pp. 1051-1058

The fundamental Vision Equation, applicable to all animals and representing the perceived brightness of the scene is:

$$\ln Y = R = K_U \text{ x } \ln \int E^*\mathbf{U} + K_S \text{ x } \ln \int E^*\mathbf{S} + K_M \text{ x } \ln \int E^*\mathbf{M} + K_L \text{ x } \ln (\int E^*\mathbf{L})^2$$

where Y is the perceived brightness, the italic term represents the illuminance of the scene expressed as a function of wavelength. The bold terms represent the absorption spectra of the respective chromophoric photodetection channels. The * in this equation indicates convolution with respect to wavelength.

The individual terms in the above equation represent the signals at the pedicles of each chromophoric photoreceptor cell.

This equation applies to the process of vision in all animals, including the tetrachromats. By eliminating terms related to unused photodetection channels, it can be applied equally as well to the two great classes of trichromats. These are the short wave trichromats found among the arthropods and the long wave trichromats found among the large chordates.

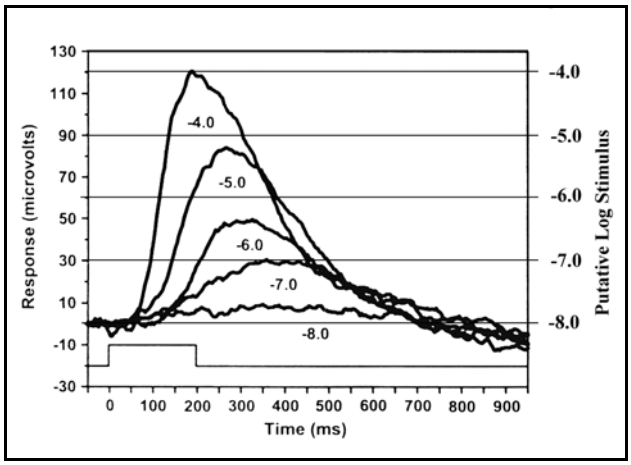

Figure 1.6.1-2 Dark-adapted zebrafish ERG responses to a 500 nm. stimulus at various irradiances. The horizontal line illustrates the onset and termination of the stimulus. Negative values below each waveform represent the log stimulus attenuation where 0.0 corresponds to a log irradiance of 15.26 log quanta per second per square cm. From Saszik & Bilotta, 1999. Auxiliary scale on right added by the author.

Based on the summation performed in the R-channel of vision, the fundamental brightness equation after decoding in the brain is given by:

$$Y(E) = e^{R(E)}$$

where Y(E) is the perceived brightness in response to the stimulus R(E) and E is the illuminance at the surface of image plane of the eye.

The perceived brightness can be presented as a function of wavelength, the Luminance Function, only after considerable manipulation of the fundamental Vision Equation. However, by using a monochromatic source and scanning it across the visible spectrum, the result, Y(E, λ), can be plotted.

By re-arrangement and considering all of the coefficients equal to one in the above equations, the form of the signals in the chromatic channels are;

$$O = \ln \int E^*\mathbf{U} - \ln \int E^*\mathbf{S} \qquad P = \ln \int E^*\mathbf{S} - \ln \int E^*\mathbf{M} \qquad Q = \ln \int E^*\mathbf{M} - \ln (\int E^*\mathbf{L})^2$$

The exponent on the long wavelength term explicitly proclaims the unique character of the Q channel. Since the difference of logarithms of two terms is equal to the logarithm of the ratio of those terms, each of these terms can be re-written as a ratio. Reintroducing the coefficients;

$$O = (K_U/K_S) \ln (\int E^*\mathbf{U}/\int E^*\mathbf{S}) \text{ etc.}$$

These equations show that the signals in the chrominance channels are ratios of chromatic content and not algebraic differences as in the Hering hypothesis.

For the long wave trichromats, the complete equation for the signal in the brightness channel is;

$$R = K_S \text{ x } \ln \int E^*\mathbf{S} + K_M \text{ x } \ln \int E^*\mathbf{M} + K_L \text{ x } \ln (\int E^*\mathbf{L})^2$$

This equation is commonly known as the Vision Equation in the literature (except the exponent is unrecognized).

These four equations define the signals transmitted to the brain via the lateral geniculate nuclei.

1.6.1.1 The fundamental equations of human vision

Since humans cannot sense light in the ultraviolet region of the spectrum, the above equations are simplified. The results appear similar to those found in the literature except for the introduction of logarithms and the square term associated with the long wavelength component. These changes are fundamental to the understanding of the visual process in humans.

The fundamental Brightness Equation for humans is given by:

$$R = K_S \times \ln\int E^{*}\mathbf{S} + K_M \times \ln\int E^{*}\mathbf{M} + K_L \times \ln\left(\int E^{*}\mathbf{L}\right)^2$$

where the coefficients are specifically those of normal human vision (no spectral adaptation).

The fundamental Chrominance Equation for humans consists of two orthogonal components given by:

$$P = K_S \times \ln\int E^{*}\mathbf{S} - K_M \times \ln\int E^{*}\mathbf{M} = (K_S/K_M) \ln\left(\int E^{*}\mathbf{S}/\int E^{*}\mathbf{M}\right)$$

and

$$Q = K_M \times \ln\int E^{*}\mathbf{M} - K_L \times \ln\left(\int E^{*}\mathbf{L}\right)^2 = (K_M/K_L) \ln\left(\int E^{*}\mathbf{M}/\left(\int E^{*}\mathbf{L}\right)^2\right)$$

In the New Chrominance Diagram to be presented in **Section 1.6.4**, these two terms are plotted orthogonally. Alternately, they can be combined vectorially into one equation, Z = P + jQ. However, this form has no theoretical or morphological significance.

1.6.2 The Spectral absorption of the chromophores

(The following discussion is restricted to the Vitamin A1 form of Vitamin A.)

Prior to this work, the precise chemistry and configuration of the chromophores of vision were not known. **Figure 1.6.2-1** summarizes the situation.

The peak at 280 nm is generally attributed to the n=π* transition associated with a carboxyl group. The peak at 325 nm is generally associated with the alcohol group in retinol. The peak at 370 nm is attributed to the aldehyde group in retinal. Although both the Vitamin A and the retinal curve are shown curving up near 300 nm, this may have been artists' license in the original art. The important point is that neither Vitamin A nor retinal shows any significant absorption at wavelengths longer than 450 nm. The waveform labeled P495 is the absorption usually associated with rhodopsin. The P495 spectrum actually represents any of four chromophores when measured in dilute solution. It exhibits two absorption peaks in the region plotted. The 280 nm peak is attributed to a carboxyl group and the peak at 495 nm is attributed to the dipolar absorption of a molecule with two heavy ligands separated by a conjugated carbon chain. These spectra are all isotropic when measured in dilute solution.

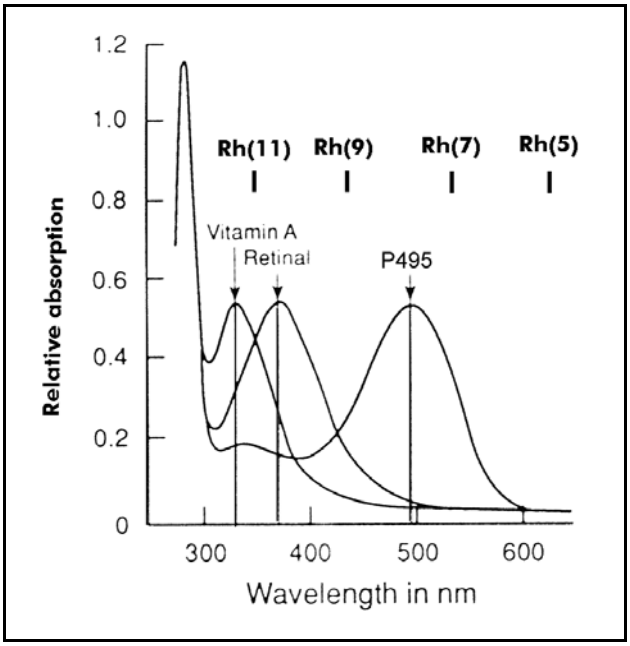

Figure 1.6.2-1 Relative absorption of various chromogens and chromophores.

The observed spectra are quite different when the materials are measured in concentrated solutions leading to the deposition of the chromophores as liquid crystals upon a substrate. The P495 material begins to exhibit an additional peak at one of the indicated values, Rh(11) at 342 nm, Rh(9) at 437 nm, Rh(7) at 532 nm or Rh(5) at 625 nm. This peak becomes the dominant peak in the spectrum. As it is deposited onto a substrate, the liquid crystalline material assumes a structured orientation and its absorption spectrum becomes highly anisotropic. **These spectra are the actual absorption spectra of the chromophores used in biological vision.** Their specific shapes of the spectra are shown in the following section. They are the spectra of the Rhodonine family of retinines, polyines derived from the polyenes of the retinene family by substitution of a second oxygen atom. The presence of the two oxygen atoms in

the polyines at separate locations represents a carboxyl ion system and accounts for the peak at 280 nm. The long wavelength peaks are the result of a slow wave mechanism associated with the specific length of the conjugated carbon backbone of the individual dipolar molecules. See **Chapter 5** and **Section 6.2**.

1.6.3 The Unified Luminance Function

This Section will employ the term luminance as equivalent to brightness to follow the previous convention. The perceived psychophysical response is actually the brightness at a specified input illuminance level.

There have been no attempts in recent years to define the actual luminance function of the human eye. The C.I.E activity has always specified the luminance function for a non-real Standard Observer. **Figure 1.6.3-1** illustrates the spectral responses of the three chromophores of long wavelength trichromatic vision and the result of combining these responses to obtain the complete luminance function. The total explanation of this figure will be presented in **Section 17.2.2.1**. That presentation is based on the equations presented in **Chapter 16**.

The Luminance Function of the Human Eye is the response to the signals from the three chromophores of vision when weighted and summed logarithmically at the pedicles of the photoreceptor cells. These signals are subject to the absorption of the incident light by the lens group before it reaches the photoreceptor cells. In the Short wavelength and medium wavelength regions, the individual signals are the integral of the incident photon flux times the absorption profile of the chromophore as a function of the wavelength. In the long wavelength region, another mechanism causes the integral to be with respect to the square of the incident photon flux. Under the nominal weighting associated with dark adaptation, the spectrum resulting from this summation, obtained using a spectral filter no wider than 10 nm, is shown by the theoretical Photopic Luminance Function in the figure. It will be shown that the C.I.E curve is the result of smoothing this curve with a nominal 30 nm filter. This was the nominal filter width of the 1920-30s when the data was collected.

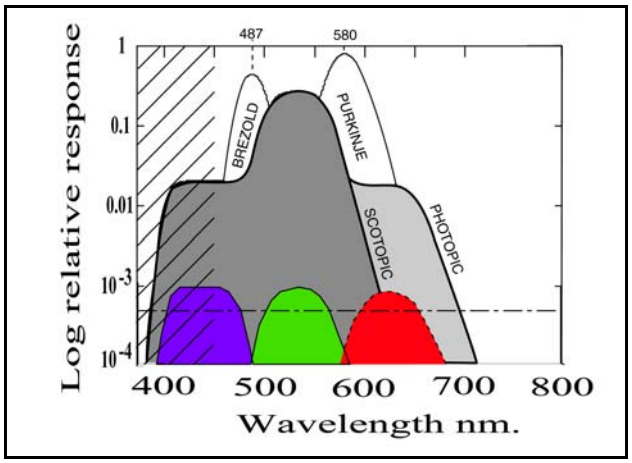

Figure 1.6.3-1 The luminance function and the spectral responses forming it.

There are many other cases of interest. If the light level is reduced, the square term in the long wavelength integral causes the response in that area to fall faster than in the other areas. If the light level is reduced considerably, the resulting Luminance Function is given by the curve labeled Scotopic. Here again, the C.I.E equivalent is obtained by smoothing the theoretical function.

If spectral adaptation is introduced, the Luminance Function will vary. The most common variation is where the long wavelength illumination component is raised relative to the medium wavelength component during sunrise and sunset. In these cases, the relative amplitude of the long wavelength and medium wavelength signals are more nearly equal after weighting. Because of the logarithmic summation, the so-called Purkinje Peak (at about 580 nm) is observed as shown in the figure. This peak is also frequently observed in the psychophysics laboratory when a low color temperature light source is used in the experiments. It is frequently misinterpreted as the peak in the absorption of the long wavelength chromophore.

A second situation occurs if the photon flux applied to the eye across the spectral band is kept constant but the eye is pre-adapted to suppress the output signal from the medium wavelength photoreceptor cells. In this case, the logarithmic summation process results in dual peaks in the overall spectrum at 487 and 580 nm although there are no chromophores with absorption peaks at these wavelengths. This dual peak situation is known as the Brezold-Brucke Phenomenon.

When the perceived brightness is plotted with respect to wavelength while presenting the luminance of the source parametrically, these various effects can be recorded. **Figure 1.6.3-2**, adopted from Hurvich & Jameson[163], illustrates these effects but suffers from experimental difficulties. Each response is displaced by one log unit for

[163]Hurvich, L. & Jameson, D. (1953) Spectral sensitivity of the fovea. I. Neutral adaptation. *J. Opt. Soc. Am.* vol. 43, no. 6, pp 485-

convenience. The graph illustrates the characteristic change in the absorption characteristic of the human eye as a function of illumination. By preparing a similar graph without introducing the one log unit displacement, the transition from scotopic to photopic vision is more apparent.

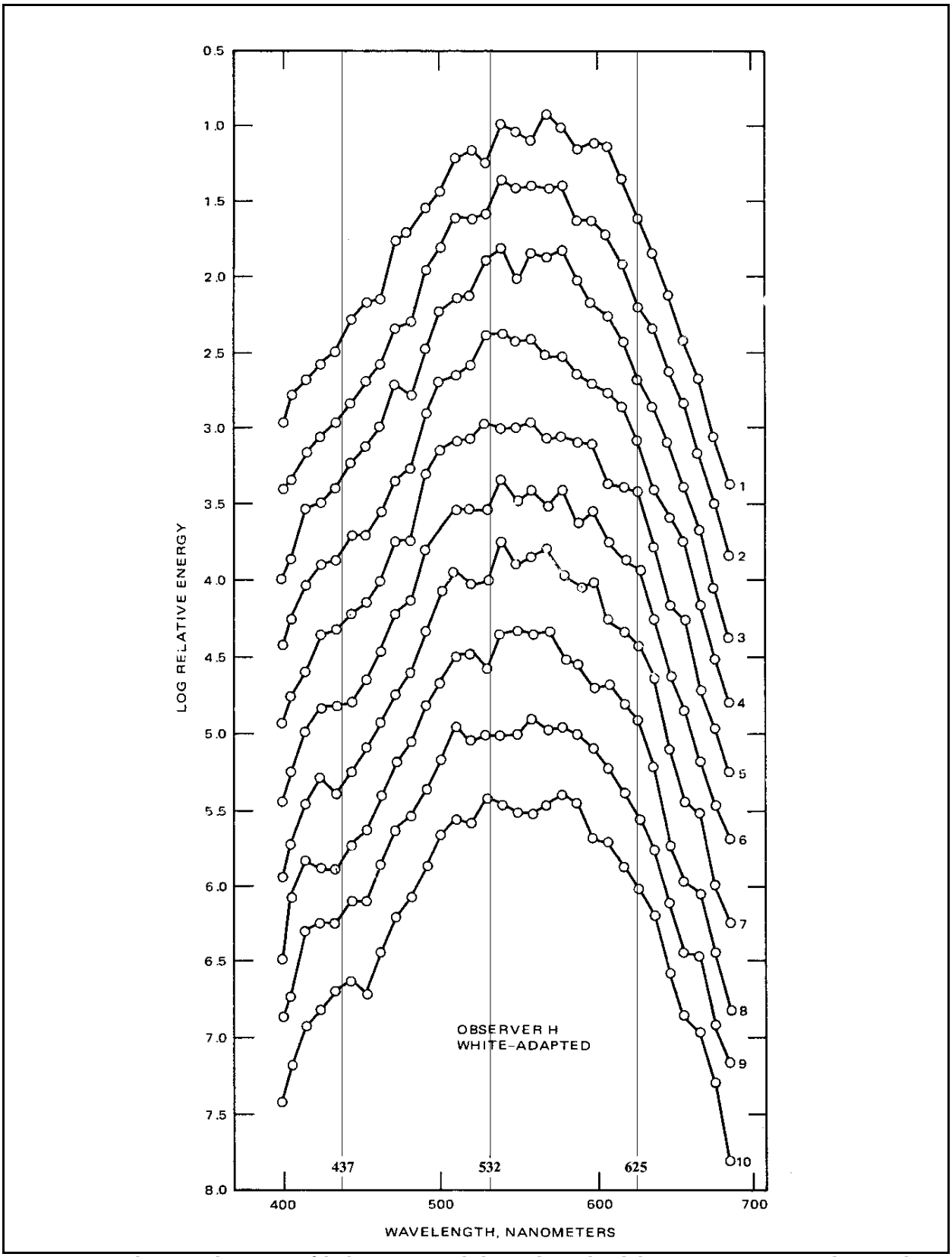

Figure 1.6.3-2 The spectral response of the human eye with the irradiance level shown as a parameter. Values are shown for the hypertopic through scotopic regions of vision and neutral adaptation. Adopted from Hurvich & Jameson, 1953.

1.6.4 The New Chromaticity Diagram

Chapter 17 will present the New Chromaticity Diagram in a three-dimensional format as it applies to tetrachromatic animals. As opposed to most earlier diagrams that applied to object space, the New Chromaticity Diagram represents **perceived** color space. There are a variety of attributes associated with this change in focus.

For humans, only a two-dimensional format is required to represent the equation Z(P,Q) = P + jQ. This Diagram is presented in **Figure 1.6.4-1**. The fundamental parameters of the graph have been chosen so that the spectrum locus of pure monochromatic lights coincides with the axes and the corner of this spectrum locus occurs at the center wavelength of the M-channel. This presentation has many advantages over previous diagrams. The basic advantage is that no real or imaginary tristimulus values are required in its construction. Only the actual absorption coefficients of the chromophores are used. There are no non-spectral colors in this presentation. Hence, there is no "purple line." All colors are represented by a two-term expression expressed in spectral wavelengths. White is represented by the expression 570, 494 nm regardless of the color temperature of the source illumination, as will be explained later. An extension of this diagram to object space shows how the various Standard Illuminants all appear to produce scenes *perceived* as containing a significant amount of white.

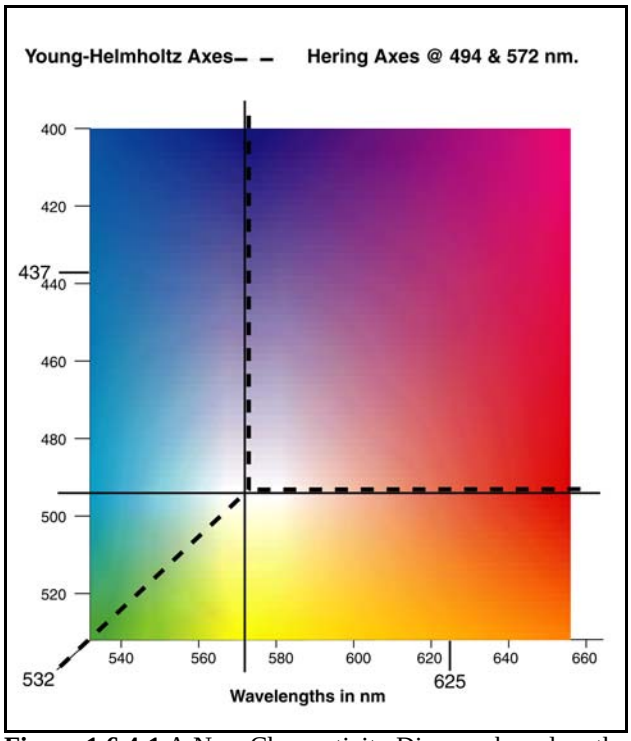

Figure 1.6.4-1 A New Chromaticity Diagram based on the orthogonality of the two chrominance channels of human vision.

1.6.5 A new theoretical wavelength discrimination function

By taking the derivative of each of the two chrominance functions, P & Q, and selecting the most sensitive one in a given case, a theoretical wavelength discrimination function is obtained. This function closely matches the experimental data and can be extended to other cases not found in the literature. **Figure 1.6.5-1** presents this graph. **(A)** in this figure is the theoretical wavelength discrimination function for a specific set of parameters based on this work. **(B)** is the equivalent data from the literature for several sets of parameters. Note the similar local minima, local maxima and inflexion points in the two frames. See **Section 17.2** for the detailed discussion.

1.6.6 A new theoretical dark adaptation characteristic

Figure 1.6.6-1 presents the theoretical dark adaptation characteristic developed in this work for a specific set of parameters. The heavy curve shows a resemblance to the previous characteristics found in the literature but is distinctly different. Historically, this characteristic has been considered to consist of two exponential functions according to an unknown underlying mechanism. This work describes the actual mechanisms and shows the result is the solution of a third order differential equation (See **Section 16.3.6**). Historically, although the data was available, the curve was truncated at about 25 minutes so the rise above the underlying exponential near 25-30 minutes did not require explanation. The solution of a third order differential equation is not the product of two exponentials but the product of an exponential and a sinusoidal term. This precise form does call for a rise above the underlying exponential and fits the actual data points better than the historical approximation. For abnormal parameters, this mathematical form also provides a precise description of several pathological conditions of vision as shown. See **Section 18.2.2**.

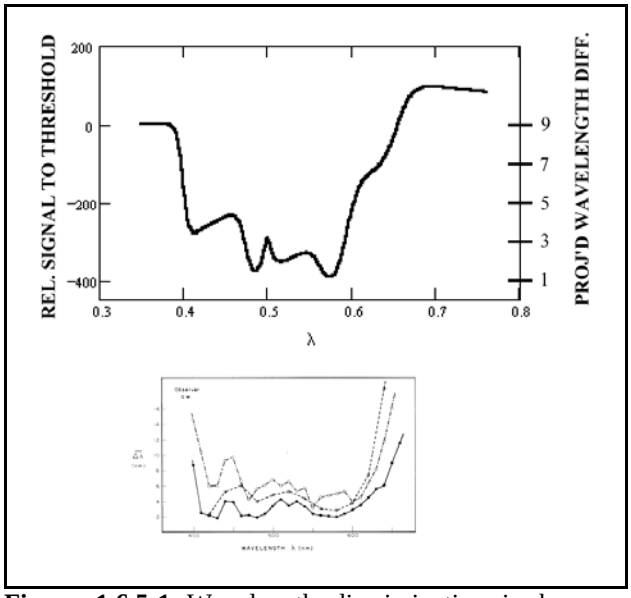

Figure 1.6.5-1 Wavelength discrimination in humans. (a)The theoretical wavelength discrimination function for normally sighted humans. (b) Experimental data for comparison

1.6.7 The Standard Human Eye of research (& associated parameters)

This work has accumulated and correlated a large variety of parameters that relate to the performance of the human visual system. These have been assembled into a single file in **Appendix L** for easy reference and to insure continuity in this work.

Appendix L, A Standardized Human Eye for Research is divided into six tabular sections;

I OPTICS
II RETINAL MOSAIC
III PHOTODETECTOR CELLS
IV SIGNAL PATH PARAMETERS
V MOTOR PARAMETERS
VI RESOLUTION PARAMETERS

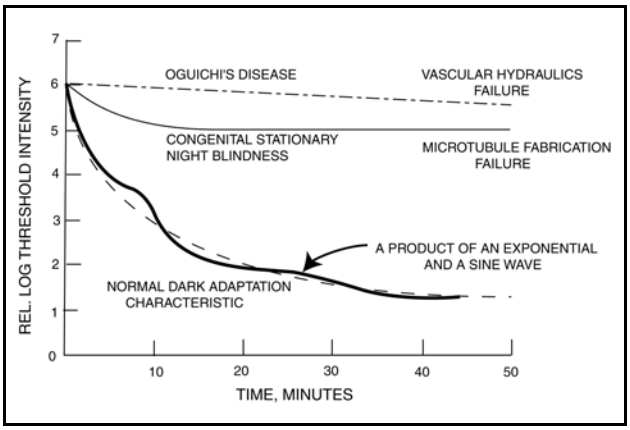

Figure 1.6.6-1 The nominal dark adaptation characteristic of human vision accompanied by two pathological conditions.

This Appendix also includes a set of detailed luminosity functions and a new chromaticity diagram. They are based on a more accurate theoretical foundation and exhibit higher precision than the widely used C.I.E. versions designed for engineering applications. These versions provide a more defendable scenario and are more appropriate for use in research.

The luminosity functions span the hypertopic, photopic, mesotopic and scotopic range. The chromaticity diagram spans the normal trichromatic range but can be expanded to include the tetrachromatic range for use in research on aphakic eyes.

Section 2.4.2 will review the physiological optical system of the human eye in detail. Hogan, et. al. provide a brief

summary of the variation in major dimensions of the eye among individuals and with age[164].

1.6.7.1 General features of the Human Eye

Summarizing the optical system of the Human eye, the following major mechanisms are observed;

+ the visual system operates as an immersed optical system

+ the main lens is the cornea; the differential lens, used for accommodation, is the element known as the lens

+ the cornea-lens combination, labeled the lens group, is an example of elliptical optical design

+ the differential lens has a graded index of refraction in both the axial and the radial direction

+ the image field of the combined cornea and lens is highly curved to match the curvature of the retina on the inside of the ocular

+ the image formed on the retina is highly distorted due primarily to the change in focal length of the combined cornea and lens as a function of field angle.

+ there is a field lens, made up of neural tissue, but its importance is minimal in human vision.

+ each photoreceptor has the potential for a collimating lens based on the structure known as the ellipsoid. If exploited, the resulting optics of the eye forms an afocal (or telephoto) optical system.

+ under extreme conditions, the RPE may act as an energy absorber for photons not absorbed by the chromophores of vision.

1.6.7.2 Previous Standard Human Eyes

Scanning the above mechanisms, a problem is quickly recognized with the various Standard Eyes that appear in the literature. First, they are limited to the optics of the eyes. These Standard Eyes were developed along with the visual sciences and without a comprehensive model to aid in the interpretation of the histological data. Using first order (Gaussian) optics was mathematically necessary in that time period. The result is that these "Standard Eyes" are generally adequate for optometric, and some ophthalmological, purposes. However, they only apply to a region within less than one degree of the centerline of the optical system (Interestingly, this region does not include the fovea). They do not address the variable focal length of the optical system with field angle. Neither do they recognize the potential afocal aspects of the actual optical system, since they do not address the role played by the ellipsoid of the Inner Segment in the overall optical performance of the human eye. Generally, they also do not address the statistical variation in the physical parameters of the human eye. Although the authors of these standards were aware of the variable index of refraction of the lens, the state of the computational art did not support performance of a complete ray-trace on a real human optical system. Similarly, specifying the variation in the various optical elements of the eye was difficult. During the 1990's, the team of Artal and associates has added significantly to the available data on the human eye. The review article of 1996 provided a comprehensive list of their, and related, works[165]. Both their work and that of van Meeteren & Dunnewold[166] appear to be based on the assumption that the eye is based on spherical optics. Allowance must be made in the use of this data because of this assumption. It is now possible to ray-trace the entire optical system on a desk top computer in less than a few hours. To continue research on the human eye, a new tabulation of the optics of the "Standard Eye" is needed.

1.7 Generic visual subsystems based on morphology

Presenting a comprehensive block diagram of the visual process before proceeding is important. This will add both specificity and clarity to the discussion and also provide a framework for evaluating conflicting theories found in the literature. **Figure 1.7.1-1** attempts to provide a high-level block diagram that can be used to place more detailed

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[164]Hogan, M. & Alvarado, J. & Waddell, J. (1971) Histology of the human eye. Phila. PA: W. B. Saunders pg 50

[165]Artal, P. Marcos, S. Iglesias, I. & Green, D. (1996) Optical modulation transfer and contrast sensitivity with decentered small pupils in the human eye. Vision Res. vol. 36, pp. 3575-3586

[166]van Meeteren, A. & Dunnewold, C. (1983) Image quality of the human eye for eccentric entrance pupils. Vision Res. vol. 23, pp. 573-579

diagrams, schematics, and models in context. An attempt has been made to adopt the terminology of other investigators where possible. However, the various designations can only be considered nominal. A similar diagram has recently appeared due to Backhaus, et. al[167]. A problem with that rendition is it does not recognize the fact that more than 90% of the neurons do not generate "graded potential or spikes." Only the arrows between their upper three boxes involve signal transmission by "graded potentials. Simpler versions of these figures, using more refined concepts, will be developed in **Section 11.1.6**.

To emphasize its chordate foundation, the figure shows the photoreceptor cell rotated as found in inverse retinas. Although this figure uses the nomenclature normally used in discussing vision in human and other chordate animals, a similar figure can be constructed for the arthropods and molluscs by rotating the photoreceptor structure and changing the labels. Many labels associated with the various arrows are the same as those used by other authors (only the code numbers defined by Polyak[168] have been specifically attributed). Stage B_2 is called photoreceptor optics by Snyder & Menzel.

The most important idea is to subdivide the overall vision process into a series of steps focused on different classes of processes, i. e., separating physiological optics from computational optics (a remapping or filtering of input information into a different context for output to a later processing element(s)). This figure has been extended into the administrative domain because of the important correlation of the work of the C. I. E. with the basic vision processes. Without considering the work of the C.I.E. in the proper context, applying their data erroneously and subsequently drawing incorrect judgments is easy.

[167]Backhaus, W. Kliegl, R. & Werner, J. Color Vision: Perspectives from Different Disciplines NY: W de Gruyter fig. 2.1

[168]Polyak, S. (1941) The retina: the anatomy and the histology of the retina in man, ape & monkey. Chicago, IL: University of Chicago Press

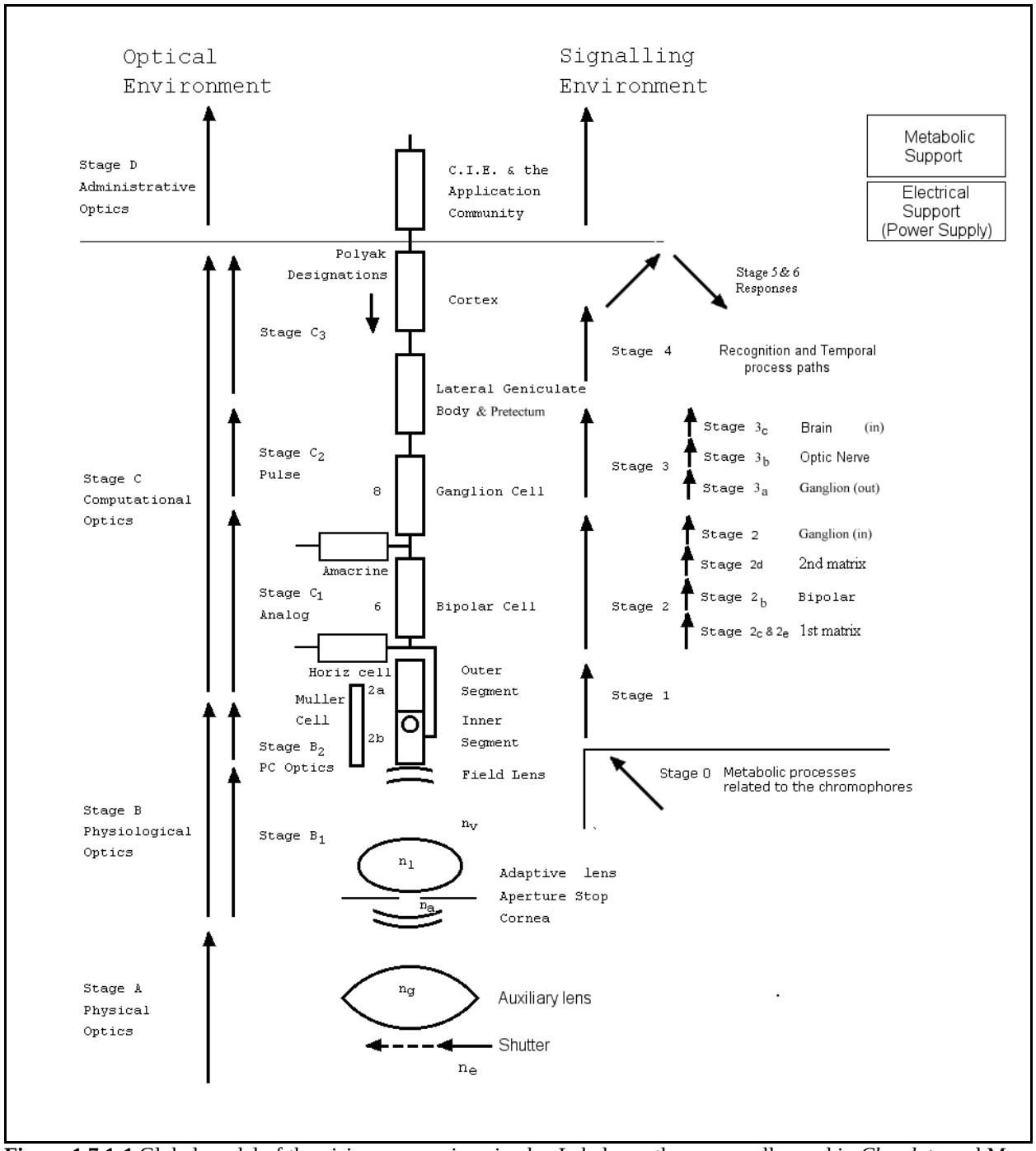

Figure 1.7.1-1 Global model of the vision process in animals. Labels are those normally used in *Chordata* and Man. Stage B2 shows a reversed retina for emphasis. The same model can be used for other animals by changing the names of the elements and rotating the photoreceptor in Stage B2.

The overall diagram is described by two sets of partitions, one relating to the optical performance of the eye and the second relating to the signal processing performance of the eye. The diagram consists of five alphabetically labeled stages (on the right) related to optics;

A--Physical Optics, B--Physiological Optics, C--Computational Optics, and D--Perceived Optics. Each of these can

be subdivided as shown on the left. As an Example, Stage B is appropriately subdivided into the physiological optics external to the Inner Segment of the photoreceptor cells, Stage B1, and the physiological optics found within the Inner Segment, Stage B2.

The indices shown correspond to the index of refraction for; vitreous humor, n_v, lens, n_l, aqueous humor, n_a, cornea, n_c, environment, n_e, and any external optics, n_g.

The physical optics of stage A can be spectacles, telescopes, microscopes, etc. It can also be used to account for the nictating lens of some animals.

The diagram consists of five numbered stages (on the right) related to the signal environment;

1. Signals found internal to the photoreceptor cells
2. Signals found in the space between the output node of the photoreceptor cell and the input to the action potential generator inside the ganglion cell
3. Signals found proximal to the action potential generator inside the ganglion cell and distal to the lateral geniculate body
4. Signals found proximal to the lateral geniculate body and distal to the initial receiving circuits in the cortex
5. Perceived responses produced by the animal and tabulated by the vision and lighting community

For convenience, Stage 2 has been subdivided into three subclassifications, 21, 22, and 23 to avoid confusion in later discussions.

Stage D and Stage 5 could both be labeled Perceived Responses or merged into one classification by that name for they make up the fundamental collection of knowledge of how the eye responds to stimuli. This knowledge consists of both the raw data in the literature and the representation of this data in an easily interpreted and usable form; the latter include the material generated by the C.I.E.

The Diagram also shows the retina of the inverse type found in Chordata for three reasons. The twisted signal path shown emphasizes the inverse nature of the retina. This is the configuration found in Man, a principal subject of this work. By simply inverting the photoreceptor cell, the diagram becomes that of any eye found in Mollusca or Arthropoda.

The nomenclature on the right has been extended into the metabolic domain by the definition of Stage 0. This stage is concerned with the very critical metabolic processes, carried out with the vascular system, to create the chromophores of vision and support the operation of the signaling system. This stage is shown in the lower right quadrant.

The following sections will address the major functional stages of vision as they appear in the major phyla. As noted earlier, Martin has shown that the phylum, *Cnidaria*, the jelly-fish and polyps, also contain eyes[169]. However, the eyes found there include a variety of unusual configurations, using parts that are otherwise generic to specific higher phyla. It could be said that *Cnidaria* contains the parts kit from which the eyes of the higher phyla are assembled.

1.7.1 Generic Optical (Visual) Systems

A detailed Investigation of the various optical systems used in vision is beyond the scope of this work. This is primarily because of the limited amount of information available on the precise surface contours and indexes of refraction of the various elements found in the eyes. Without this information, only general conclusions can be drawn concerning the performance of the eyes.

Land & Nilsson have recently provided a text reviewing the wide variety of physiological optics employed in biological vision[170]. It is highly recommended. However, it does not proceed beyond the physiological optics stage and its mathematics is limited to simplified situations and the paraxial case.

1.7.1.1. Specific features

1.7.1.1.1 Optical features

[169]Martin, V. (2002) Op. Cit.
[170]Land, M. & Nilsson, D-E (2002) Animal Eyes. Oxford: Oxford University Press

Before leaping into a discussion of optical systems, reviewing the terminology is advisable. The visual systems of some animals are complex, more complex in terms of technology than most man-made optical systems (excepting some mult-function and multi-spectral systems found in military tanks). Here, complexity is measured in terms of the technologies used and the way they are integrated, not just in terms of the number of finite elements present. A variety of optical elements are used in animal vision, both imaging and non-imaging. Most texts do not differentiate between these adequately.

The animal eye achieves a level of quantum efficiency only recently equaled by man. This has been in the field of silicon-based semiconductor physics. He is still attempting to reach it in the field of silver-halide-based semiconductor physics. The problem relates to the limited absorption coefficient of most absorbing materials compared with the optical beam dispersion associated with an optical system designed to capture as much light as possible. In high performance silver-based film reconnaissance systems, this problem is one of the dominant design criteria and is plotted on a graph designed to separate the two factors effectively and allow tradeoffs to be made between them. In silicon-based systems, the arts of submicron photolithography and ion implantation allow the production of retinas with capabilities mimicking the animal vision systems.

The dispersion angle of a simple lens system is the basis for the expression, *f*/#. In simplest form, the *f*/# is defined as the focal length of the lens divided by its diameter. However, the optical pupil of the complex eye is smaller than the apparent pupil observed externally. The dispersion angle is the angle formed by the limiting ray of the optical bundle and the optical axis. This angle is typically given by dividing the diameter of the lens by twice its focal length. Because of the dispersion of a lens, the depth of focus of a typical lens is measured in microns. The formula for the depth of focus at the image plain is $\pm(\lambda \times (f/\#)^2)$ in microns. The depth of field of the human eye at the fovea is about 10 microns at 500 nm, whereas the length of the OS is about 30-50 microns. Without additional features in the optical system, most of the light brought to focus at the entrance of the photoreceptor cells would be lost before it was absorbed within the length of the OS. To operate efficiently in an imaging application, an absorber must have a high enough absorption coefficient to absorb all of the incident radiation from the lens within a distance of a few microns. Unfortunately, an absorber with this high an absorption coefficient exhibits an index of refraction that is much higher than the material in the space between the lens and the absorber. The large index change at the interface causes a very high coefficient of reflection to exist at this surface; a disastrous condition for purposes of vision, and imaging in general.

The eye has employed several techniques to resolve the above conflict;

+ by separating the imaging (light collecting) function and the dispersion control function.

+ by providing space with a low index of refraction between rows of chromophoric material in the optically absorbing region, the rods in Arthropoda and the disks of Chordata.

The dispersion control elements are given several different names in different animals including most frequently crystalline lens, ellipsoid, and oil drop. These labels have been based primarily on morphological rather than optical grounds. The spacing of the rods and disks at distances small with respect to the wavelength of the incident radiation means the radiation sees an average index of refraction that is tolerable at the entry point.

By separating the light gathering and the dispersion control tasks, the animal eye has achieved very good optical performance in an exceedingly compact system.

1.7.1.1.1.1 Imaging elements

In optical imaging systems, three types of optics are found;

+ dioptric elements which are refractors

+ catoptric elements which are reflectors

These can be assembled into systems known as dioptric, catoptric or catadioptric systems, the last consisting of both types of imaging elements.

1.7.1.1.1.2 Non-imaging elements

Non-imaging elements include several forms of waveguides;

+ the generally cylindrical element that relays optical energy from its entrance to its exit by means of total internal reflection at its cylindrical surfaces.

+ the generally cylindrical element that relays optical energy from its entrance to its exit by means of a graded index of refraction in its core material.

The latter form of a waveguide is finding wide use in fiber optic cables because of its low attenuation losses. The former form of a waveguide need not exhibit a reflective coating on its surface. A change of index between the surrounding material and the core of the waveguide can cause total internal reflection.

All of the above elements and combinations are found in various (and most) animal eyes. It behooves the investigator to recognize this fact. It is particularly important to recognize what is not obvious. As in other cases, the morphologist may say only a pigment surrounds a crystalline cone in an ommatidium. The optician would say the crystalline cone in an ommatidium is surrounded by a material of lower index of refraction leading to total internal reflection; and, oh-by the way, the surrounding material seems to be colored. The functional difference between these two observations is significant. The presence or absence of a pigment in the area surrounding a crystalline cone may or may not have any impact on the overall optical performance of the assembly. Performance is affected by both the index of refraction and the spectral absorption/reflection of the surrounding material.

> The above comments are particularly relevant to the discussion of superposition eyes in Arthropoda (See **Section 1.7.1.2.3**).

1.7.1.1.1.3 A Luneberg lens versus an oil drop

Chordate eyes employ an optical element near the entrance to the photosensitive element. These are usually refractive elements designed to recollimate the incident radiation. They are frequently labeled ellipsoids or "oil drops." Under sufficient magnification, it is seen that they are not drops in the normal sense of the word. The external surface of the drop is not smooth due to the surface tension of the material involved. The surface is actually quite rough and jagged[171]. Since this surface is so rough when observed at dimensions of less than a wavelength of light, the element can be considered a Luneberg lens. A Luneberg lens achieves an average index of refraction in a given region by using an assembly of materials of sub-wavelength dimensions and different local indexes of refraction. The material of the lens may or may not form a chromatic filter.

Because so many investigators want to believe, the oil drop is a spectral filter, it would be nice if there were large quantities of data confirming this supposition. Jacobs[172] is the only author I know who has provided the spectral response of two "oil drops." However he did not provide any provenance, even to the type of animal. **Figure 1.7.1-2** reproduces his graph.

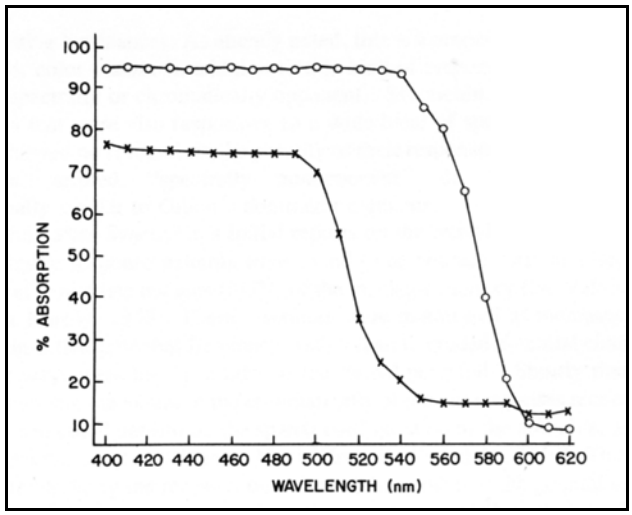

Figure 1.7.1-2 Absorbance curves for two different classes of colored oil droplets. The x–x curve corresponds to a nominal "minus blue" filter. Scenes viewed through it would appear greenish-yellow. Scenes viewed through a filter corresponding to the o–o curve would appear red. From Jacobs, 1981.

1.7.1.1.2 Environmental features

It is very important to note that in the terrestrial eye, the index of refraction of the air exterior to the eye is quite different from the index of the vitral fluid filling the eye. These eyes are operating in the immersion mode; as in an immersion microscope. The main effect of this fact is that the simple lens laws do not apply. A light ray passing through the principal point of the optical system does not pass straight through the lens system unless it is "on axis." Any other ray is diffracted according to Snell's Law. This means that the angle associated with a ray in object space is not equal to the angle of the same ray in image space. Experimenters must be clear to describe the reference condition when they speak of angles from the optical axis of the eye; are they referring to object space or to image space? The notion of the nodal point was developed to simplify this problem. However, this notion only applies to Gaussian Optics, i.e., the paraxial condition. The definition of the nodal point

[171]Rodieck, R. (1973) The vertebrate retina. San Francisco, CA: W. H. Freeman & Co. pg. 192
[172]Jacobs, G. (1981) Comparative Color Vision. NY: Academic Press, pg 43

does not extend to the off-axis optical condition.

In the marine eye, the index of refraction of the water exterior to the eye is nearly the same as the index of refraction of corneal material and to the material between the cornea and the lens. In this situation, the cornea has negligible optical power.

Some animals living in or frequently crossing the water/air interface have developed very sophisticated optical systems for maintaining vision in both environments, as will be discussed below. Although these physical adaptations have not received much attention in the literature, they are fascinating examples of the divergence employed to satisfy environmental conditions. They include;

+ use of a split aperture containing two different lenses, mounted side by side in the four-eyed fish,

+ temporary introduction of an auxiliary lens (spectacles?) in many mammals and birds, and

+ use of two separate optical forms within the available physical envelope in *Pecten*, including introduction of an entirely new optical form to animal physiology--a catadioptric lens system.

1.7.1.1.3 Mechanical features

The method of mounting the lens to the surrounding structure is important. In most animals this is via muscular tissue. The contraction of this muscular tissue can have at least two effects. It can move the lens along the optical axis compared with the other optical elements or it can stretch the lens causing it to change its shape. Movement along the axis can have two interrelated effects. Simple movement in the absence of a second optical element, as happens with most aquatic animals, will simply lead to a change of focal position and provide accommodation. Movement of one lens along the optical axis when associated with a second optical element, like the cornea in terrestrial animals, can provide a variable focal length optical system (a “zoom” optical system) and vary the focal position.

The method of mounting the lens also affects the nature of the lens itself. Whereas man found it simple to build optics based on spherical surfaces, usually called “spherical optics,” this is not the common form used in physiological lenses. Attachment of the ligaments to the lens is not accomplished at a single point along the edge of the lens. It involves a region along the edge. This causes the lens to be elliptically shaped and to change this elliptical shape when stretched by the muscle. The operation of the eye is thus based at least partly on “elliptical optics.” Analysis of the eye must accept this fact.

> Essentially all of the dioptric optical elements in the animal kingdom are elliptical optics. This is because of the method used to form them. This applies specifically to the element frequently labeled the crystalline cone in *Arthropoda*. The crystalline cone is functionally a prolate ellipsoid in many species and must be treated as such to understand the optics of those arthropod eyes.

Until recently, man did not manufacture optical materials with a variable index of refraction within a single element at all; he strove for the most homogeneous possible index of refraction in his materials. Only recently has it become possible to manufacture materials with a controlled variable index. Fiber optic cables are an elementary example but much more is being done, led by the University of Rochester. Physiological lenses exhibit a large variation in the index that must be recognized in any analysis of the eye.

1.7.1.2 The Optics of *Arthropoda*

The diversity of eyes among Arthropoda, principally *Insecta* and the Crustaceans, is astounding. Some species, particularly among the spiders, show a wide range of optical forms even within a single species. **Figure 1.7.1-3** shows the eight eyes of a wolf spider, *Lycosa*, to place their visual system in perspective. Quoting Land et al[173]., "Their eyes are divided into two initial categories, the principle or primary eyes (also described as the anterior median eyes) appear black as they lack a tapetum, have their rhabdoms distally located, and are the only eyes known to mediate polarotaxis, but others show peirpheral polaization sensitive responses."

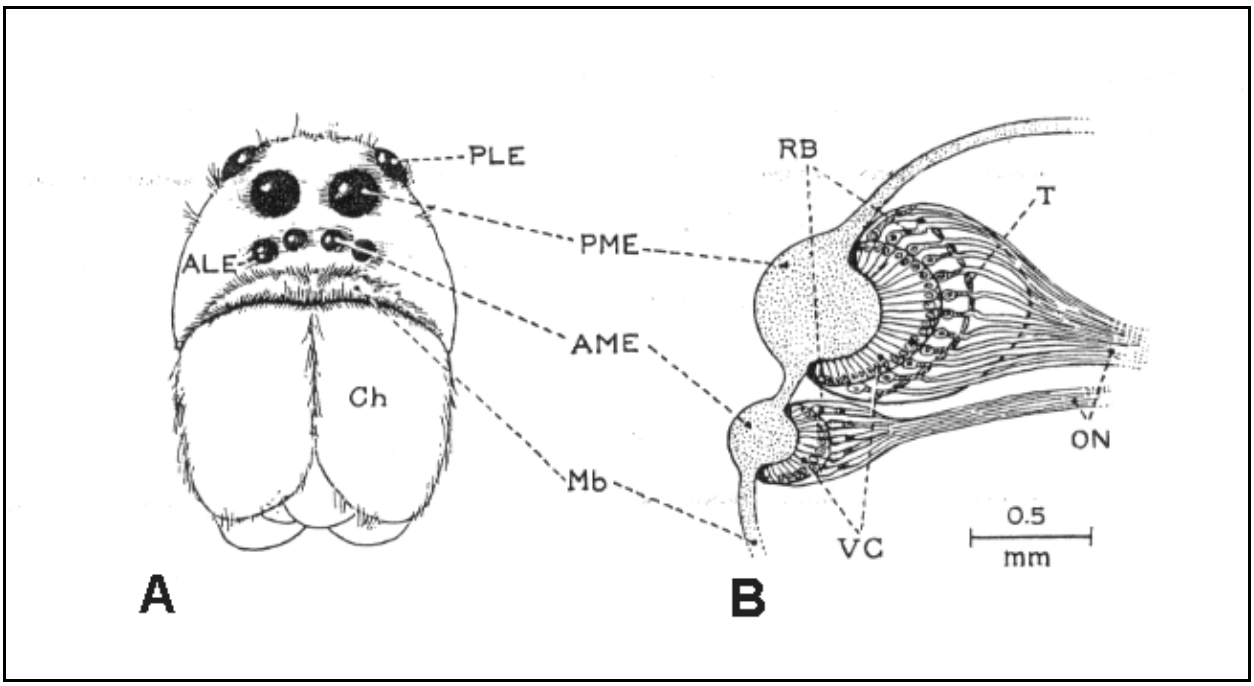

Figure 1.7.1-3 Structure of wolf spider (*Lycosa*) eyes. **A**; Frontal view of the head showing four pairs of ocelli (AME, anterior median, ALE, anterior lateral, PME posterior median, and PLE, posterior lateral). Mb; arthrodial membrane, Ch, chelicerae. **B**; Diagram of AME and PME as seen in parasagittal section. Rb, rhabdoms, VC, vitreous cells, T, tapetum and ON, optic nerves. Note the lack of a tapetum in the AME. Adapted from Land et al., 1981 and credited to DeVoe et al, 1969.

1.7.1.2.1 The simple eye

It is necessary to carefully defining the "simple eye" before proceeding. Conflict exists in the literature defining a "simple eye." Some simple eyes appear to include a lens system and some apparently do not. The case of the Limulus is an example; most authors say that Limulus has two pairs of eyes, all on its carapace; i. e. its dorsal side. A few authors speak of a light-sensitive organ on the ventral side of Limulus (on the head?). This eye is even said to be enclosed within an olfactory blood vessel. Is this an eye? Is it merely one or more cells that are light sensitive along with other properties? Many animals exhibit light-sensitive structures that may be in the process of evolution; some are rudimentary and some are archaic--such as the penial eyes of some lizards. To be considered a simple eye in this work, one or more photoreceptors must be present in conjunction with an opaque enclosure (Latin: camera) that has a single aperture forming an optical axis with the photoreceptors. The aperture may be filled with a variety of optical elements.

A photodetector that lacks an enclosure will be called a photospot instead of an eyespot to avoid misinterpretation. The next more complicated photodetector will include an optical element that operates as a light guide or an image forming element, even if there is only one light-sensitive element behind it. This fundamental configuration will be

[173]Land, M. Laughlin, S. Nassel, D. et al. (1981) B: Invertebrate Visual Centers and Behavior I *In the series*, Autrum H. *ed*. Comparative Physiology and Evolution of Vision in Invertebrates. NY: Springer-Verlag

defined as an ommatidium. If an ommatidium operates independently, it will be named an ocellus. It is the ommatidia that can be replicated and closely packed to form a compound eye.

With the aid of [**Figure 1.2.1-8(a)**], extracting the features used in the ommatidia and in the "unit eye" of the compound eye of the insect is possible. Usually, no eyelid or nictating lens is seen. A cornea and a lens are observed although the cornea may be very thin. An iris may or may not be a histologically recognized element; its importance would be small in a very narrow field of view system as found in the simple eye. The ommatidium involves only a small cluster of photoreceptor cells located behind the focal surface. The field plate if present would be an extremely simple feature, probably just a filter element. An ommatidium usually has a long focal length lens compared with the diameter of the optical system. Therefore, the *f/#* of the system is quite high. The system has an essentially fixed focal length. Little or no accommodation is provided or required. The optical element between the lens and the photoreceptor cells is usually described as a light pipe because of its high refractive index compared with its surroundings. The situation is actually more complex as shown in Land & Nilsson[174]. They show five different variation in the index of refraction between the lens and the photoreceptor capsule used to meet the needs of different species.

[**Figure 1.2.1-8(b)** & **(c)**], shows that the arrangement of the photoreceptor cells of the ommatidia is complex. At least some elements of the structure are formed so that they can sense the polarization of the incident light in at least some spectral channels.

1.7.1.2.2 The compound eye

The compound arthropod eye is just a cluster of ommatidia from an optical point of view. Additional neural functions may be present at the rear of a compound insect eye but these are separate from the optical system. The literature speaks of compound eyes where the corneas and/or lenses appear to have fused into a single structure. These fusions lead to a compound eye that is converging on the complex eye (with a direct retina) found in Mollusca.

1.7.1.2.3 Apposition versus Superposition

There is discussion in the literature concerning whether the ommatidia of a compound eye are optically isolated from each other, either permanently or diurnally. The subject is interesting but the available data is circumstantial at best. Most of the discussion relies on cartoons.

If the ommatidia are optically isolated, the result is called an apposition type of compound eye. If the walls between the ommatidia are sufficiently transparent, and of the appropriate index of refraction to avoid a waveguide effect, light from multiple adjacent lenses may be focused on a single photoreceptor element. This is the mode of operation found in the superposition type of compound eye.

The possibility also exists that the apposition type of compound eye could employ computation to achieve the signal integration feature provided by the optical superposition type of eye. Operation in this form would employ a two-dimensional photoreceptor array in each ommatidia and a slight overlap of the field of view of adjacent ommatidia. By cross-connecting the photoreceptors having the same field of view, increased sensitivity could be achieved. Here, a more complicated apposition eye would form a computational-based superposition eye and perform like an optically-based superposition eye.

Changing from an optical apposition to an optical superposition type of eye on a diurnal basis would require a mode change in the computational circuits supporting the visual process.

The details related to apposition and superposition types of optical systems in Arthropoda are not very important to this work, are quite controversial, and will not be explored further. Two papers review this subject area[175],[176]. Land & Fernald take pains to explain the conceptual operation of the putative superposition eye using a series of cartoons instead of optical ray traces.

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[174]Land, M. & Nilsson, D-E. (2002) Animal Eyes. Oxford: Oxford Univ. Press, pg 132

[175]Land, M. & Fernald, R. (1992) The evolution of eyes. in Annu. Rev. Neurosci. vol. 15. pp. 13-20

[176]Snyder, A. (1979) in Comparative physiology and evolution of vision in invertebrates. Autrum, H. ed. NY: Springer-Verlag pp. 228, also Miller, pp. 72-73

1.7.1.3 The Optics of *Mollusca*

The eyes in this Phylum take on a very wide variety of geometric forms. A prototypical form of the retina for this Phylum is shown below in [**Figure 1.7.2-1.**] These eyes are all basically body mounted and consist of many direct photoreceptor cells in the focal plane of a single optical system. One of the simplest eyes in this Phylum is that of the developmentally primitive *Nautilus*, class *Cephalopoda*. This eye has an "iris" but no rigid structure analogous to a lens or cornea. The retina may be exposed directly to the fluid of the animal's environment or a more viscous fluid may be secreted to seal the opening mechanically. Lacking any viscous fluid with a different index of refraction than sea water, the eye is analogous to a pinhole camera. This most simple eye appears to show a functional similarity to the heat sensors of the snake family.

The more advanced eyes in this Phylum contain millions of photoreceptors behind adaptable optical systems providing overall sensitivity and resolution approaching that found in the chordates. Only limited data has appeared on the spectral response of the octopus. Messenger[177] found only one chromophoric pigment in its eye with a peak wavelength of 475 nm. This value causes the data to be suspect for two reasons, the spectral response graph shows several inflection points typical of a multi-spectral eye and several references appear in the literature as to the polarization sensitivity of the octopus eye. It is most likely that further documentation will show the fundamental mollusc eye enjoys tetrachromatic capability with polarization sensitivity in at least one spectral region.

Jagger & Sands[178] have recently presented a gradient index optical model of the eye of the Octopus. In their discussion, they highlight a pupil (aperture stop) between the two lenses (their anterior and posterior lenses) and an adjustable iris external to the anterior lens. They show that the lens group acts almost as one spherical lens with the index of refraction of the material varying radially from a single center. The index is nominally 1.50 at the core of the lens group to nominally 1.36 at the cortex. The spherical form of the lens group provides a very wide field angle. They suggest there is strong phylogenic convergence between the optical system of the eyes of two visual predators, the octopus of *Cephalopoda* and the brown trout of *Pisces*. They also review the resolution capability of the eye as a function of the shape of the iris. Jagger & Sands provide several references to additional data.

1.7.1.3.1 Dual focal planes and retina

The mollusc, *Pecten*, has evolved a capability that is difficult to describe in a section on either optics or retinas. Because of the unique environment occupied by this animal, it has developed an eye that is probably unique also. Although the fact that it has two retinas within a single eye has been described histologically often beginning in the 1880's, its operation has not been explained before. The retinas have usually been described as back to back based on histology. It will be shown that they are both direct retinas based on optics.

Land[179] explained, early in his career, how part of the optics worked but missed the overall solution. The solution is tailored to the fact that the animal lives in the tidal zone and must be able to see when immersed in water or when surrounded by air. It cannot control the time when each of these environments exists. Therefore, it has evolved an eye that can operate in either environment at any time. The eye has two image planes. One is created by a dioptric assembly and is used when the animal is surrounded by air. A second, formed by a catadioptric assembly, is used when surrounded by water. **Figure 1.7.1-4** is an expansion of Land's Text-fig. 5. **A** shows the optics of the eye when immersed in sea water as depicted by Land. **B** shows the same optical system when operating in air. Note the paradox, the eye in air is of the immersed optical type while the eye in water is of the non-immersed, or conventional, optical type. C is a photograph from Land showing the cross section of the actual eye for comparison.

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[177]Messenger, J. (1981) Comparitive physiology of vison in molluscs. *In*, Handbook of sensory physiology, vol. VII/6C, Autrum, H. *Ed*. Berlin: Springer-Verlag pp. 93-200

[178]Jagger, W. & Sands, P. (1999) A wide-angle gradient index optical model of the crystalline lens and eye of the octopus. Vision Res. Vol. 39, pp. 2841-2852

[179]Land, M. (1965) Image formation by a concave reflector in the eye of the scallop, *Pecten maximus*. J. Physiol. (London) vol. 179, pp.138-153

Note that both images are facing the same direction. Land also provided details of the two retinas that will be discussed in a later section. In a later paper, Barber et. al[180]. have shown additional details of the retinal arrangement. As seen from the optical perspective presented here, **B** is clearly the original dioptric optical assembly. **A** is an adaption using the reflective material represented by the argentea (tapetum) as an imaging element of a second optical assembly. Land has noted the high optical collection efficiency of the catadioptric design. He calculates an *f*/# = 0.6. using a net catadioptric focal length of 0.850 mm based on a dioptric focal length of 1.238 mm., S. D. = 0.470 mm. in sea water. The calculated dioptric focal length in air would be about 0.92 mm. Although the dioptric assembly has a slightly longer focal length, it is still optically fast. The overall optical efficiency is reduced by the fact that in both cases, the unfocused light passes through one retina on the way to its focal surface. Since these eyes are both change detectors, the loss of contrast due to the undesired absorption of light destined for the other retina is not a serious problem.

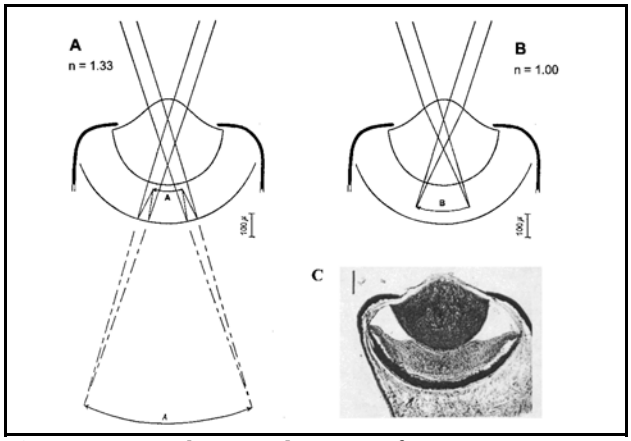

Figure 1.7.1-4 The optical system of *Pecten maximus*. A shows the catadioptric system used when the animal is submerged. B shows the dioptric system used when the animal is in air. C is a micrograph of actual eye cross section. All scales 100 microns. The two focal plane positions are marked as upper case A and lower case a. Frames A & C from Land 1965.

As will be seen more clearly in a later section, the two retinas are both illuminated from the same side from an optical perspective.

1.7.1.4 The Optics of *Chordata*

Figure 1.7.1-5(A) presents the generic optical system for Chordata. This system is used in a variety of families occupying different niches. The entire assembly is mounted on a two degree-of-freedom ocular platform controlled by three pairs of muscles. This arrangement allows rapid changes in the direction of fixation.

The generic chordate eye includes two "eye lids" and many animals use both of them. Man uses the first eye lid as a shutter. The second one is not used but some investigators claim it is present in rudimentary form. On the other hand many semiaquatic animals, both mammalian, reptilian and avian, use both eye lids. One acts as a shutter and the second acts as a nictating lens. This lens allows the animal to compensate for the optical ineffectiveness of the cornea when the animal is submerged in water. Other chordates apparently use the two eyelids redundantly for added protection against damage to the eye.

In terrestrial animals, the cornea is the strongest optical element in the chordate eye, the "lens" operates only as a weak variable focal length lens. The variable focal length feature is controlled by the Precision Optical System of the midbrain. It varies the net focal length of the optical system (accommodation) in order to maintain focus for objects at different distances from the optics.

The position of the iris between the cornea and the "lens" and the fact that the "lens" is made from a material with a graded index of refraction is very important; the combination provides the high degree of curvature required for the projected image to focus on the inside of the ocular. It is also important in maintaining the *f*/# of the optical path nearly constant regardless of field angle. The Stiles-Crawford effect is a direct result of this configuration. When the iris is wide open, the variable index of the "lens" causes a variation in the optical path difference (OPD) between the scene and the image for rays passing through different zones of the lens.

The optical characteristics of the cornea, iris, "lens" combination provides a very wide field of view system, as high as 180 degrees in object space and approximately 100 degrees in image space. However, the wide field of view and the highly curved image plane necessarily leads to very high geometric distortion in the image. Fortunately, the distortion approaches zero for small images near the optical axis of the system. Guyton[181] failed to recognize this distortion in his Figure 60-6. His presentation implies that the image on the retina is an accurately scaled copy of the

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[180]Barber, V. Evans, E & Land, M. (1967) The fine structure of the eye of the mollusc *Pecten maximus*. Z. Zellforsch. vol. 76, pg. 295

[181]Guyton, A. (1976) Textbook of medical physiology. 5th ed. Philadelphia, PA: W. B. Saunders pp. 815-816

object, a large black cross. He then says that the pattern transmitted to the cortex is also an accurately scaled copy of the object. Neither of these situations is true for a finite size object. As will be seen later, his assertion that it is the contrast transitions at the edges of the cross that are most important in signal processing and perception is correct.

Immediately behind the focal plane and in front of each individual OS is a small collimating lens placed within the IS and usually labeled the ellipsoid. This component is very important in maximizing the sensitivity of the overall eye. Without this element, or some alternate device, the light impinging on the OS would be out of focus over most of the length of the OS. This would result in a very great loss in perceived image contrast. The OS does act as a light pipe but this does not alleviate the problem because the light pipe has only a limited acceptance angle. This small angle is due to the small difference in index of refraction between the OS and the surrounding Inter-Photoreceptor-Matrix (IPM). See **Section 4.3.4**.

1.7.1.4.1 The nictating lens

Any animal that is a transient between the aquatic and the terrestrial environment must have a solution to the difference in the index of refraction between the two environments. This is commonly accomplished using the nictating lens solution. It is found in diving birds, and also reptiles such as the crocodile, which operate in both environments at different times.

1.7.1.4.2 The four-eyed fish

One animal has found a unique solution to the multi-environment problem that meets its ecological needs. The four-eyed fish, *Anableps tetrophthalmus*, is accustomed to swimming at the water's surface and hunting simultaneously in both the aquatic and terrestrial (air above the water) environment. Thus, it operates in both the aquatic and terrestrial environments simultaneously and the nictating eyelid is not an entirely satisfactory approach. It has capitalized on the features of the variable index nature of the lens to solve its problem, with a possible loss in some field of view. **Figure 1.7.1-5(B)** shows its solution. By rotating the axis of the elliptical lens compared with the optical axis, it compensates for the loss in optical power of the cornea when looking under water. Rays from below the water pass through the much more curved (higher optical power) part of the lens while the rays from above the waterline pass through the less curved (lower power) part of the lens. The result is that both rays encounter essentially the same focal length optical system and both come to a focus in a single contiguous focal surface. This solution may encounter some displacement of the focal surface at the junction of the two fields of view. This is where it quite possible the field plate will be important as discussed below. The field plate can compensate for small focal surface discontinuities.

Recently, a more primitive form of four-eyed fish has been found. Bathylychnops exilis has been described by Cohen as having two separate oceli on each side of its head with the minor eye looking downward, perpendicular to the axis of this ancient fish shaped like a pike[182].

1.7.1.4.3 The field plate

The field plate, known in conventional photography as the field lens or the field flattener, is a more complex device in the eye. It more closely relates to a combination of a spectral filter combined with a meniscus lens to form a very finely detailed focus correction plate.

Especially near the fixation point of the eye, the field plate is frequently colored, called the macula lutea in this region, and acts as a "minus blue" filter. This is frequently described as eliminating a large amount of glare light similar to the effect of minus blue hunting glasses. However, it is obviously not totally effective in humans or hunting glasses would not be so spectacular in their performance and would not sell well.

A field plate can be looked upon as a meniscus lens very near the focal plane that can provide a significant amount of correction for chromatic aberration. This could be a compensation for the chromatic aberration due to the remainder of the optical system. The variable thickness of the field plate can, and does, cause a change in the position of the focal surface and/or a change in magnification. This feature can be used for several purposes.

It is believed that the field plate, in some hunting birds in particular, is shaped to provide additional magnification of the image in the immediate region of the fovea. This effect is illustrated in **Figure 1.7.1-5(C)**. The sharp curvature of the first surface of the field plate causes a bending outward of the ray bundles near the visual axis. The detail in

[182]Cohen, D. (1958) *Stanford Ichth. Bull* vol 7, page 47

the image traverses additional photoreceptors of the retina, resulting higher resolution in the object plane than normally calculated based on the focal length of the optical system alone. Snyder & Miller have analyzed this effect and provided measurements of its significance in these hunting birds[183]. They show that these birds achieve a magnification of about 1.45 times that of an equivalent size human eye. This leads to a detectivity, at a distance, as much as 8:1 higher in these equivalent size bird eyes than in human eyes. As Snyder & Miller noted, their "fig. 2 represents only a crude model of the optics." It would be better to show the negative lens of the field plate as a plano-concave lens, with the flat surface toward the photoreceptor, and to show the oil droplet as a spherical element at the image plane if that is their supposition. An alternate supposition will be explored in **Section 2.4.6**. It is shown there that the oil droplet is probably behind the Petzval surface.

It is occasionally claimed that the same magnifying effect is found in the human eye. However, **Figure 1.7.1-5(D)** shows the similar situation in the human eye. In the human eye, the diameter of the thinned portion is about 600 microns. The change in curvature is much lower that in the eyes of birds reported in the literature. Significant magnification would not be achieved in this situation. It is more likely that the thinning of the field plate near the fovea is related to the desire to achieve maximum resolution by moving the various neural bodies out of the optical path in this region.

[183]Snyder, A. & Miller, W. (1978) Telephoto lens system of falconiform eyes. *Nature*, vol. 273, pp 127-129

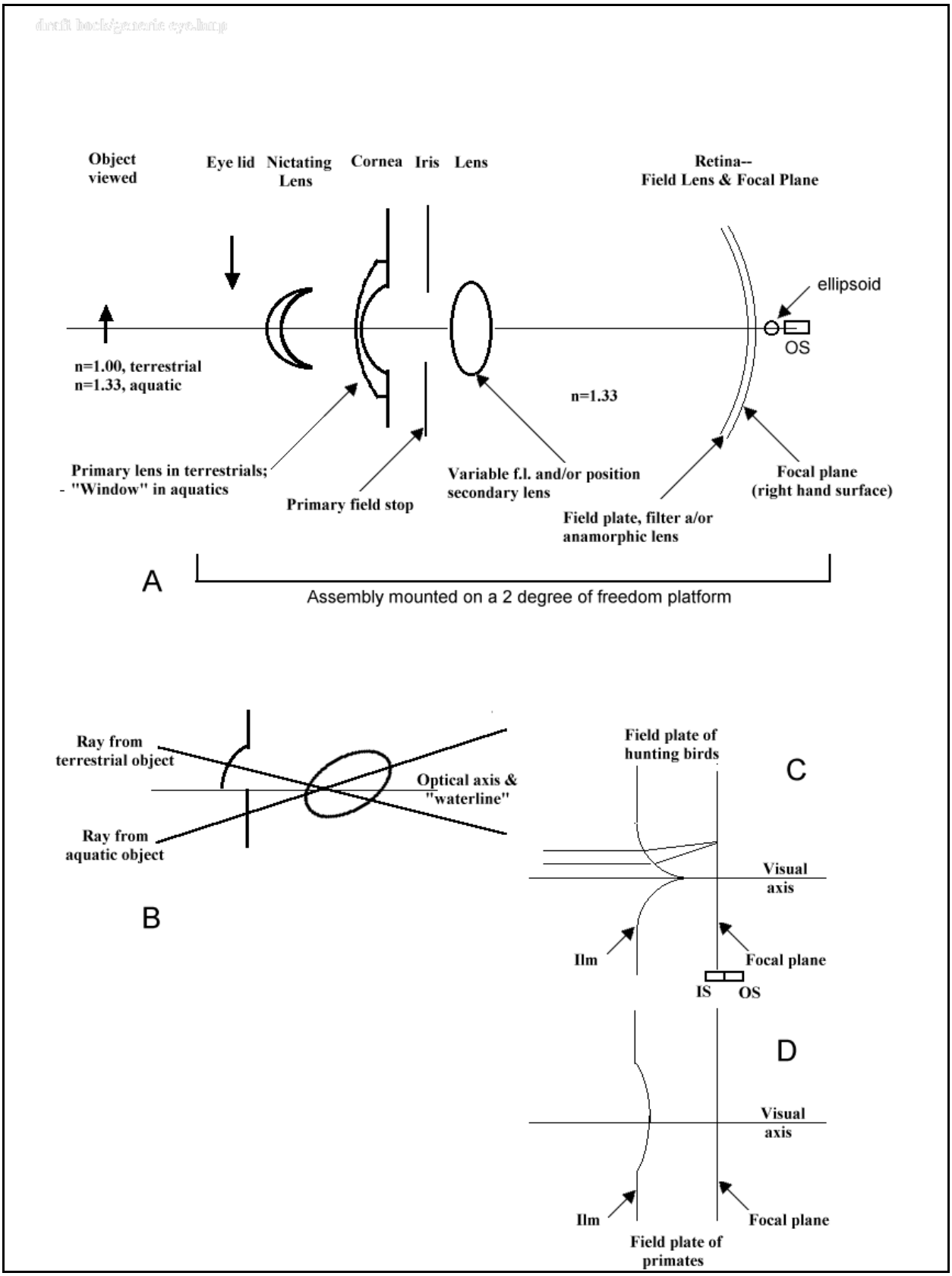

Figure 1.7.1-5 The Generic Eye of *Chordata* and some of its modifications

Note before proceeding that the depth of focus in an optical system, using the human as an example, is only a matter of 10 microns each side of the focal surface. No matter what local changes in focal length may be caused by the field plate, the surface describing the location of (or the entrance to) the active portion of the photoreceptors must follow the contour of the focal surface within about +/-5 microns. This requirement is frequently overlooked in histological work. The curvature in this nominal surface near the foveola can be seen clearly in **Figure 1.7.1-6**.

Franze et al. have recently proposed the neural tissue of the retina forms a fiber optic plate instead of a simple meniscus lens[184]. They describe their plate as dominated by radial Mueller cells, that funnel the light through the neural tissue efficiently while allowing room for other neural tissue. They suggest these Mueller cells account for the cobblestone-like appearance of the inner surface of the retina. They did not provide any figures describing the optical system of the eye based on their proposal. The Petzval surface (the focal surface formed by the light) of the optical system (including at the foveola) would be of particular relevance to their concept, as would a more detailed drawing of how a single Mueller cell was shared between one cone and approximately 10 rods (their number). They did not describe the capture angle at the input surface or the maximum exit angle of the fiber optic plate. To be effective it would necessarily have an acceptance angle of at least 45 degrees to support operation of the retina at 90 degrees from the fixation point (see Append L, the Standard Eye). The light from the pupil is arriving at 45 degrees from the surface of the neural tissue at this point. Franze et al. did include considerable index of refraction data for the neural tissue but not the photoreceptor cells. Their approach can be compared to the following approach using the inner segments as wide angle lenses.

1.7.1.4.4 The Inner Segment

With or without a field plate, matching the highly converging optical bundle formed by the main refractors of the human eye with the long slender Outer Segments (OS) of the photoreceptors is a problem. In the absence of an additional optical element, much of the incident light will not be absorbed by the chromophores located behind the point of best focus. In addition, the light that is not absorbed must be prevented from reaching the chromophores in adjacent disk stacks. Failure to absorb all of the available photons will lower the sensitivity of the eye and light reaching adjacent chromophores will result in a loss in perceived contrast.

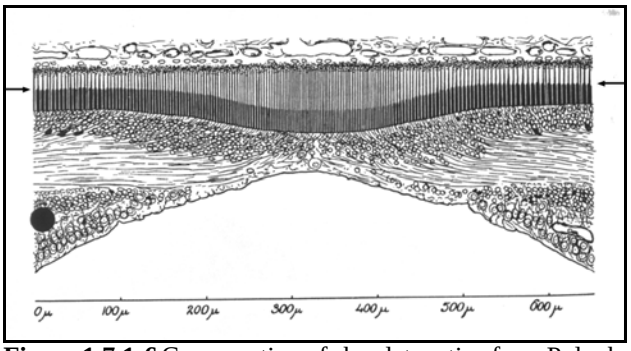

Figure 1.7.1-6 Cross section of chordate retina from Polyak, 1941. Arrows added to indicate the location and shape of the focal surface. Note the considerable curvature in the area of the foveola required to accommodate the magnifying effect provided by the neural layer acting as a field plate.

Two solutions to the above problem present themselves. Rodieck[185] has presented material on the optical properties of the Inner Segment (IS). The discussion then focuses on the possibilities of the IS acting as a light pipe. Although the IS might be a light pipe, the difference between its average index of refraction and that of the fluid surrounding it is small (0.024); the acceptance angle of such a light pipe is small. The ellipsoid, found in the IS of the photoreceptor cell, and the tissue surrounding it offers a different solution to the above problems. The difference in index of refraction for these two materials is larger, 0.04, and a different mechanism is used. **Figure 1.7.1-7** describes the optical conditions and shows how the problem is solved. The ellipsoid has a higher index of refraction than the surrounding tissue, is only a few wavelengths of light in diameter, and has a diameter similar to the entrance aperture of the OS. To a first order, the ellipsoid will act as a spherical lens. If placed slightly beyond the focal plane of the main optics, it will act as a collimator. The resulting combination of the main optics and the collimator forms a telephoto system. This configuration is also known as an afocal telescope of the astronomical type. The light from a distant point arrives at the main optics in a parallel beam and the light leaving the telephoto system is also in a parallel beam. Thus, the light passing into the OS is collimated. Its degree of collimation is higher than the acceptance angle of the OS when considered a light pipe for all wavelengths of interest. The light is thus constrained to stay inside the OS until it is absorbed or until it reaches the end of the OS. This mechanism raises the sensitivity of the eye significantly under low light level conditions when the iris of the eye is fully open. It probably accounts for the significantly higher sensitivity of the retina compared with silver halide film, a factor of at least 10:1. When the iris is closed, the mechanism is still operative but it is less importance. Under this condition, it is

[184]Franze, K. Grosche, J. Skatchkov, S. et al. (2007) Muller cells are living optical fibers in the vertebrate retina PNAS vol 104(20), pp 8287-82982

[185]Rodieck, R. (1973) The vertebrate retina. San Francisco, CA: W. H. Freeman & Co. pp. 145-150

not needed to increase sensitivity since the eye is not expected to achieve high sensitivity. The mechanism is still effective in maintaining perceived image contrast.

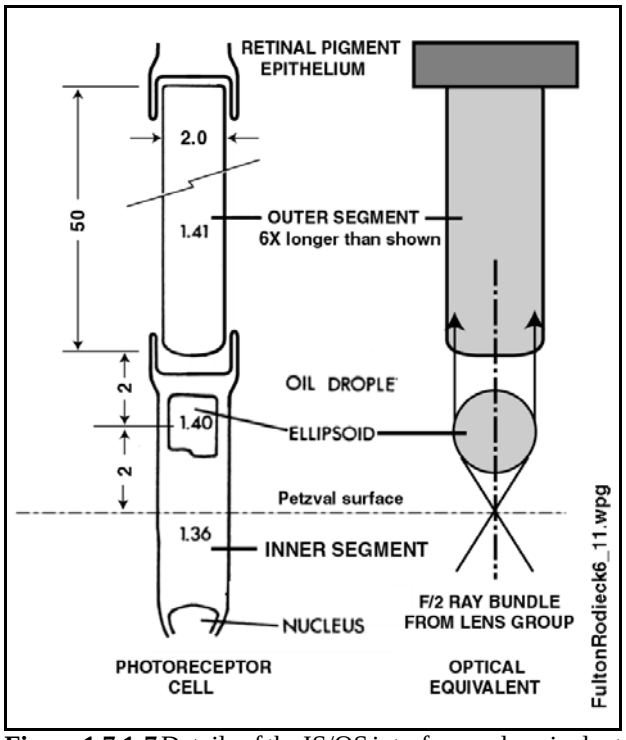

Figure 1.7.1-7 Details of the IS/OS interface and equivalent optical diagram. All dimensions in microns. Note foreshortening of OS. Index of refraction of surrounding fluids, 1.336

1.7.1.5.1 Cursory examination

The focal length of an inverting afocal telescope is equal to the sum of the focal lengths of the main lens group plus the focal length of the collimating element.

1.7.1.5 Comparison of the Optical Systems in Vision

Summarizing the above discussion with a composite figure showing a variety of common features and trends found in the animal optical system is useful. **Figure 1.7.1-8** presents such a composite of caricatures for purposes of comparison. It is in the style of Wolken but includes iconic versions of previous figures in this work. The individual caricatures have been created from a review of the work of many experimentalists. Many of these workers were attempting to illustrate a specific point. Only by combining the work of several can an appropriate caricature be obtained for each phylum. However, the responsibility for the features shown is entirely that of this author. The figure can be compared directly with a similar composite by Wolken (1975, fig 13-1)

The labels in the caption are meant to be from the vernacular until adopted more formerly in the next Section.

After reviewing the following subsections, seeing the evolutionary trifurcation in the visual systems of animals is easier. It also becomes easier to understand the additional modifications found within individual species.

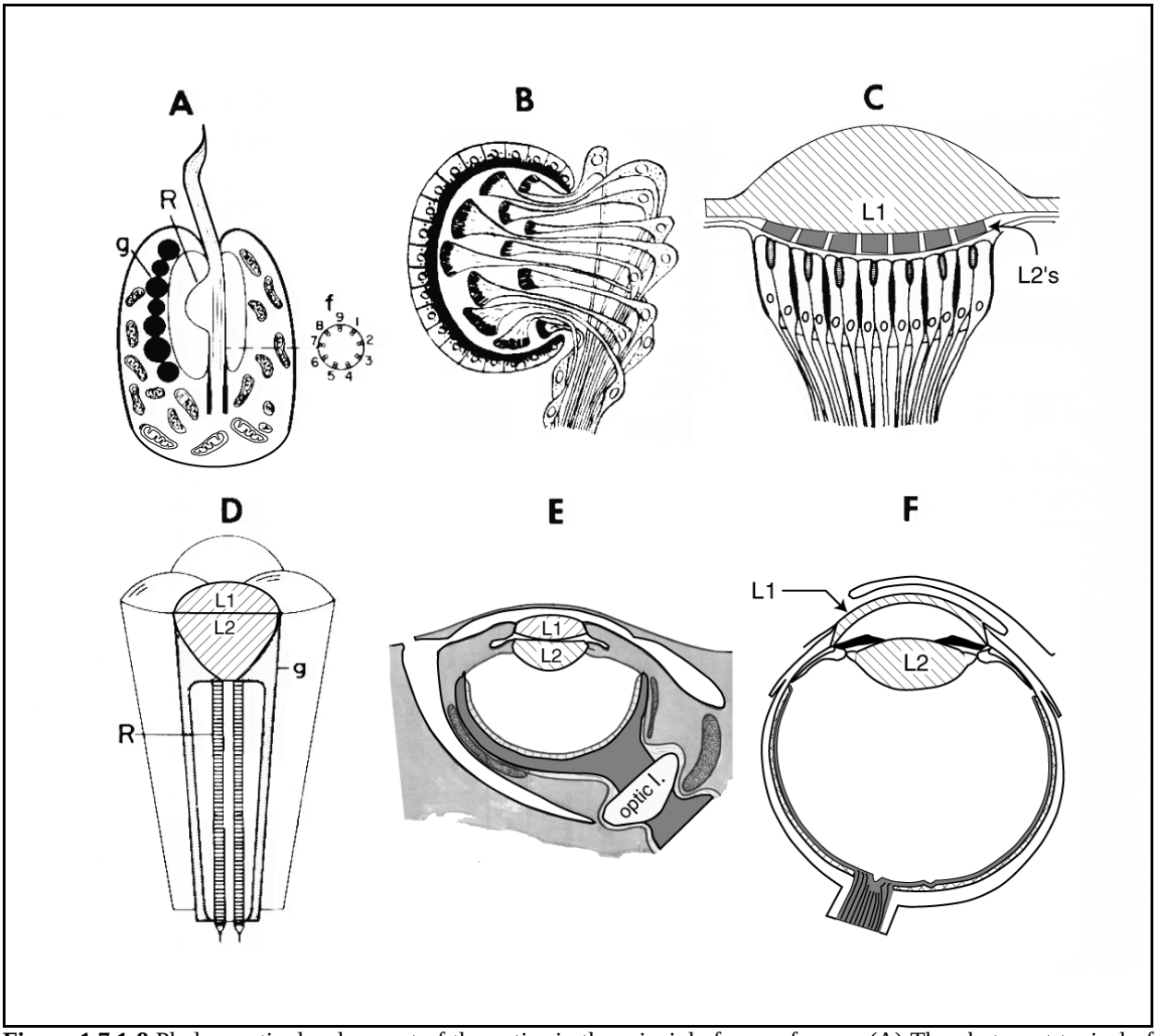

Figure 1.7.1-8 Phylogenetic development of the optics in the principle forms of eyes. (A) The photospot typical of primitive animals lacking a plane of symmetry, e.g. *Euglena*. (B) The photospots of the earliest bilateral animals, e. g. *Planaria* (still lacking a lens). (C) The ocellus or simple eye found in *Arthropoda*. (D) The compound eye found in *Arthropoda*. (E) The complex eye with direct retina found in *Mollusca.* (F) The complex eye with reverse retina found in *Chordata*. See notes for details. Layout following the plan of Wolken (1975)

(A) shows a typical photospot of early animals without a plane of symmetry, and typical of the Protozoa, *Euglena*. Note that this figure shows the entire animal. The top of the caricature ends in a flagellum. In this case, there is a series of retinula arranged around a neural pathway and "guarded" by a series of pigment granules (g) apparently exterior to the retinula (r) and their rhabdomeres. The neural pathway contains nine separate dendrites or branches of dendrites. Nine is a common number for these initial neural channels in eyes. It is the number found in man at a similar location. *Euglena* is known to turn in response to illumination. It appears that the pigment granules act as an *optical stop* along an optical axis formed by the granules and the center of the rhabdom. When light passes around both sides of the pigment granules, it excites the retinula symmetrically. However, if the illumination is asymmetrical, the neural signals from the rhabdom causes the muscle of the flagellum to cause the animal to turn until a balance is restored.

> Differentiating between pigment granules and chromophoric material is important in the remainder of this work. Pigment granules is a common designation for any opaque material in biology. The material may be opaque due to absorption or reflection of light. It may also be colored or black. Chromophoric material has a more specific definition. It is a material that absorbs light of a

> specific spectral range very efficiently and responds to that radiation by raising one or more of its electrons to an excited state. Some material labeled pigment granules may be chromogenic, such as that found in the RPE. Other pigment granules may be used to form the camera associated with an eye or photospot.

(B) is a photospot found in the simplest bilaterally symmetrical animals such as *Planaria*. It still lacks a lens. However, the "C" shaped rows of cells are pigmented and raised above the surface of the animal and form what an optician calls a *knife edge*. Since the animal is bilateral, it has two of these photospots. The multiple sensory cells and the knife edge associated with each spot allow for sensing simple movements of a source of illumination by differential shadowing. There is no imaging or directional location at the photosensor level.

This work adopts the requirement that an eye must have an optical aperture, generally filled by a lens. Photosensitive systems without an optical aperture are considered photospots and not eyes. This is significant in categorizing photosensitive areas found in throats, on tops of various skulls, etc.

Looking ahead briefly, the portion of (D) shown in cross section is defined as a single ommatidium. It consists of three principal parts. The two optical elements marked L1 and L2 and the sensory apparatus known as a rhabdom. This latter element is complicated in its own right and generally acts as a light pipe in order to optimize absorption of the desired radiation. (C), (D), (E) & (F) all include elements marked L1 and L2. It may be the rule that all fully developed eyes in the animal kingdom contain at least two lens elements in series. The location of these lenses can vary considerably. A significant criterion is whether the two lenses are in contact with each other or separated by a significant distance. There is a similar criterion about whether the second lens is next to or separated from the photosensitive structure.

(C) is the first figure exhibiting a complete eye. It is the simple eye or ocellus found throughout *Arthropoda* and much of *Mollusca*. The *aperture* is shown filled by two lenses. The surrounding light shield of the *camera* is not shown explicitly. The shield consists of pigment granules both surrounding the entire eye and between the ommatidia. As indicated earlier, this simple eye results from the replication behind a single anterior lens (the cornea) of an assembly consisting of a single rhabdom and posterior lenses (crystalline cones) of an ommatidium. Note the two lenses are adjacent and the second lenses and rhabdoms are adjacent. Although not obvious, this eye can have a considerable field of view. The distal lens presents a considerable amount of optical wedge to each assembly of an anterior lens and a rhabdom. The result is a broad fan of individual fields of view. The eye is not an imaging eye. Creation of an image occurs in the signal processing following the eye.

(D), (E), & (F) can be considered phylum specific. (D) is found predominantly in *Arthropoda*. (E) is found in the higher species of *Mollusca* and (F) is the only current eye in *Chordata*.

(D) is the compound eye of Arthropoda. By sectioning this eye through one of its fundamental optical assemblies, all of the elements of an individual ommatidium can be clearly seen. Here again, the rhabdomeres form a retinula shielded from light from adjacent optical assemblies by pigment granules. The extent of these granules is widely reported in the literature to be a variable (leading to apposition and supposition types of compound eyes). This type of eye is clearly formed by the replication of an entire ommatidium. Each ommatidium contains one rhabdom, one anterior lens and one posterior lens. The posterior lens is usually a prolate ellipsoid in form although it may have more flattened ends in some situations. As hinted above, the two lenses need not be next to each other. They may be separated by a (tapered) structural tube.

As in (C), the two complex eyes shown in (E) and (F) are not replicated from a complete ommatidium. Instead, the retinal portion is a replication of only the photo-sensors found in an ommatidium (with various degrees of precision depending on species) behind one group of optical elements grouped in the *aperture* of the *camera*.

> It is tempting to use the term "one dioptric system" when discussing the optical system of an animal. However, this term is not entirely appropriate and not completely correct for most eyes. A dioptric system is an entirely refractive image-forming optical system. The so-called crystalline lens (gel lens) in many *Arthropoda* appears to act as a reflecting light pipe. Some members of *Mollusca* employ a true catadioptric system. It also appears that many mammals employ a phase retardation plate formed by the signal processing neurons of the retina. Such an element is not image forming and is not properly classified as dioptric.

Note in (E) that there are two optical elements shown. The upper lens, L1, could rightfully be described as the corneal lens and the lower lens, L2, can be considered an oblate ellipsoidal lens. Whereas Wolken shows the anterior lens group as a single element, most other authors show, or can be interpreted as showing, a two lens group.

Brusca & Brusca[186] show a two lens group. Hegner[187], based on Hensen from Parker & Haswell provide a caricature showing a deep fissure between the two halves of what could be considered either a single lens or a two lens group. Barnes, et. al.[188] speak of a cornea and lens, show two distinct elements and two distinct call-outs but use the singular form lens for the anterior group in their illustration. There is also a substantial membrane shown passing over the cornea and covering the aperture in (E). This feature is also shown variously, and usually in inadequate detail, by the above authors. Brusca & Brusca and Barnes et. al. label it the cornea. Hegner & Engemann label it a "false cornea." Nesis[189] labels it a secondary cornea in *Myopsida* and a secondary eyelid in *Octopoda*. It is clearly separate from the epidermis forming the outer shell of the eye. Several of these authors also show an iris in front of the anterior lens group. See particularly Jagger & Sands who define both an external iris and an internal aperture stop[190]. Boycott & Young also show a distinct iris on the external surface of the external lens[191]. An external iris would be less than optimally placed from an optical perspective. A second aperture stop in this position, with a conventional aperture stop between the lenses, would cause substantial vignetting of the peripheral field of vision. The photoreceptors of the retina of Mollusca are directly illuminated. There is no neural material between the incoming illumination and the photosensitive material.

The eye of *Chordata* (F) shows many similarities to that of *Mollusca*. L1 is the corneal lens and L2 is known commonly as the "lens." (F) also shows a substantial membrane passing over the cornea and covering the aperture. This is not the common bifurcated eyelid of man but a nictating eyelid used for many purposes in different species of *Chordata.* Although not commonly show n in sketches by man, the eyes of *Chordata* typically exhibit a second or nictating eyelid. The role of this eyelid is discussed in the next section. It is residual in the highest primates.

The primary design differences between the eye of Chordata and Mollusca are two. *Chordata* exhibits a reverse retina. The photoreceptors of *Chordata* are only illuminated after the light has passed through the neural network of the retina. This network must be nearly transparent and optically non-scattering if satisfactory operation is to be obtained. Second, the ocular globe of Chordata can rotate through at least a small angular range. This makes it easy to change the line of fixation of the eye. This feature is key to the overall imaging capability of the visual system in the higher chordates. Note that in the higher members of Mollusca, the eye has evolved to the point where it can rotate slightly. It can oscillate over a small angle about a point located between the retina and the optic lobe. The angle of this rotation is adequate to support the imaging requirements of the eye.

The birds of prey and the bottlenose dolphin (and possibly others) exhibit a unique feature among Chordata. It appears that the socket for their eyes provide the capability to rotate from a side-looking to a forward-looking orientation.

The eye orientations of the *falconiforms* is shown in Section 2.4.2 (Figure 2.4.2-9) of **Chapter 2**. To more fully support forward vision, the *falconiforms* have also evolved a retina with two distinct foveola.

An example of the excellent forward looking, and likely stereoscopic, vision in this orientation is found in a video in the National Graphic video archive[192]. It shows the dolphins off the southern tip of the Everglades National Park capturing local fish as they jump into the air to escape a hunting maneuver by the dolphins. They capture most of the fish in a head-on encounter obviously requiring good forward vision. The bottlenose dolphin is able to reorient both its hearing and vision to a forward-looking orientation at low speeds, as shown in **Figure 1.7.1-9** and in Figure J.2.1-2 in **Appendix J**. At higher swim speeds, both modalities are side-looking due to streamlining requirements.

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[186]Brusca, R. & Brusca, G. (1990) Invertebrates. Sunderland, MA: sinauer Associates, Inc. pg. 750

[187]Hegner, R. & Engemann, J. (1968) Invertebrate zoology, 2nd Ed. NY: Macmillan pp. 272-273

[188]Barnes, R. Calow, P. & Olive, P. (1988) The invertebrates. London: Blackwell Scientific Publications pp. 168-169

[189]Nesis, K. (1987) Cephalopods of the world Neptune City, N.J. : T.F.H. Publications, pp. 74-77

[190]Jagger, W. & Sands, P. (1999) A wide-angle gradient index optical model of the crystalline lens and eye of the octopus. Vision Res. Vol. 39, pp. 2841-2852

[191]Boycott, B. & Young, R. (1956) Reactions to Shape in Octopus Vulgaris Lamarck *Proc Zoological Soc London* vol126(4), pp 491-547 https://doi.org/10.1111/j.1096-3642.1956.tb00451.x

[192]https://www.nationalgeographic.com/tv/shows/americas-national-parks/episode-guide/season-01/episode-10-olympic--everglades/vdka10732779

Figure 1.7.1-9 Forward-looking orientation of Dolphin eyes. When swimming at high speed, the eyes are rotated to be primarily side-looking.

1.7.1.5.2 Auxiliary features

All three of the phyla of interest have taken precautions to prevent damage to the exterior of the anterior lens. In the relatively short lived members of Arthropoda, a thin layer of cellular material is formed over the lens surface. The material hardens and is frequently labeled a cuticle. Short hairs may also be emanating from the junction between the individual corneas. In the generally longer life members of *Chordata*, the thin layer (about five layers of cells) is formed of squamous cells. These cells are both replaceable and able to move across the surface. They also support an extremely thin (~7 microns) aqueous layer that may be liquid-crystalline in form. In engineering, these cells and associated aqueous layer play the role of a dry lubricant like graphite. Although these cells are derived from the epidermis and are coplanar with the mucous surface of the conjunctiva at the junction of the two, they are functionally and constitutionally different. These extremely thin protective layers have no optical significance. The conjunctiva is much thicker. Oyster[193] discusses the external structure of the cornea of human in some detail. No data was found in the literature about the outer cells of the anterior lens of *Mollusca*.

To protect the eye against more substantial damage, both *Mollusca* and *Chordata* use a more substantial transparent covering that is more closely related to the conjunctiva. Whether this eyelid covers the aperture of the cornea at a given time is frequently under nervous control. In the case of amphibians and also birds and mammals that cross the air-water interface frequently, this auxiliary transparent membrane is frequently transformed into a nictating auxiliary lens to compensate for the change in index of refraction of the environment external to the eye. It may be the feature labeled a false cornea by Hegner & Engemann in some *Octopus* is such a modified eyelid.

As indicated above, the neural matrix of the reverse retina is in the optical path of the chordate eye. This offers another optimization not available in Mollusca. By tailoring the thickness of this neural layer, increasing the acuity of the eye over a limited geometric area is possible. In the mammalian eye, the result is generally a fovea behind the thinnest part of this optical field plate. In birds, the optimization is more complex, frequently resulting in multiple fovea at different locations.

The shape of the anterior lens of the animal eye is determined almost entirely by its nominal environment. In *Mollusca* the anterior lens tends to be thick because the index of refraction on each side of it is nearly the same. The same situation is found in the aquatic forms of *Chordata*. In these species, the posterior lens is frequently the one of greatest optical power. Fritsches, et. al. have provided a cross-section of the eye of a large swordfish[194]. The interior lens is spherical because of the wide angle of view desired and the fact the index of refraction is the same on both sides of the lens. The outer lens is essentially a powerless meniscus acting as a liquid barrier. The central optical ray travels straight through this type of lens. As a result, the angle formed by the internal cavity behind the lens is the same as the maximum field of view outside the eye.

In the terrestrial forms of *Chordata*, the situation is quite different. Although the anterior lens appears less imposing, it becomes the optically stronger of the two because of the great difference in index of refraction between the two sides of this lens. If the eye of a terrestrial animal is to image properly under water, major modifications must be made to the optical prescription of the eye to compensate for the presence of a fluid on both sides of the anterior lens. This is frequently done by introducing a nictating lens that has evolved from the nictating eyelid. Although not researched in detail, there are reports that certain insects of *Arthropoda* have compensated differently when under water. They carry along a bubble of air covering their head. This does not allow them to breathe under water. They do not breathe. However, it aids their vision.

1.7.1.5.3 Fields of view & degrees of freedom

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[193]Oyster, C. (1999) The human eye. Sunderland, MA: Sinauer Associates, pg. 352

[194]Fritsches, K. Brill, R. & Warrant, E. (2005) Warm eyes provide superior vision in swordfishes *Current Biology* vol. 15, pp 55-58

Each Phylum uses an eye covering a very wide field of view, typically more than 180 degrees. In *Arthropoda*, this large field angle is obtained using a highly replicated compound eye that is hard mounted to the head or body of the animal.

In *Mollusca* and *Chordata*, the wide field of view is obtained by using a very sophisticated anterior lens group. The lenses are classed as elliptical in optical design and the equivalent man-made group is frequently labeled a "fish eye lens." This label is entirely anecdotal in origin and technically inappropriate.

Appropriate positioning of the eyes with regard to the head and body can provide significantly different total fields of view. Pirenne shows the visual and blind zone for the human and other primates. He also shows the visual field for birds (in plan view) and notes the absence of <u>any</u> blind zone[195]. This lack of any significant blind zone is typical of many other species.

The retinas of the eyes in (E) and (F) are fundamentally different and can be traced back to the evolutionary fork in the road taken at *Planaria*. The retina in (E) is typical of *Mollusca* and is body mounted to the animal. In this configuration, as in *Arthropoda*, there is little structural flexibility between the eye and the body of the animal. The neurons exit the eye in a relatively large diameter bundle. No ganglion cells have been found in these eyes that could provide a reduction in the size of this bundle. In (F), the reverse retina of Chordata provides a capability not shared with the other Phyla. The retina is designed to encode the data from all of the photoreceptors into a much smaller number of neural channels. Fewer channels lead to a smaller and more flexible optic nerve. This greater degree of flexibility is a great advantage in changing the angle of fixation of the eye independently from the head. This flexibility is also beneficial in converting the eye of Chordata from a starer to an imager. A tremor is easily introduced. The more advanced members of Mollusca share this ability to employ a muscular tremor to provide imaging. In (E), the eye is nearly completely isolated from the head. Introduction of a muscle between the two dark cartilagous elements on the right in this figure allows introduction of tremor but not free rotation. The pivot point for the tremor is in the middle of the narrowest part of the optic nerve bundle leading to the optic lobe of the brain.

The human eye exhibits more freedom of rotary motion than most other mammals. It exhibits three degrees of freedom; it can rotate over a significant angle in both the horizontal and vertical planes, and to a lesser degree, it can rotate about the line of fixation to accommodate proper image orientation on the foveola as discussed in the next paragraph.

1.7.1.5.4 Image orientation

There are many references in the literature to the fact that the image on the human retina is inverted and reversed, a feature of any combination of lenses that do not exhibit an intermediate focal plane. All of the imaging optical systems of animals, such as (E) and (F), exhibit this feature. This characteristic is irrelevant in vision since the signals extracted from the image by the retina are not used to reconstruct an equivalent image in the brain. Even the few photoreceptors of the foveola connected directly to the Pretectum are not directly concerned with the orientation of the image, only its contrast edges. The Pretectum extracts these details and passes them to the higher cerebral regions where the content is determined independent of orientation. Many experiments have shown that the nominal orientation of an object is determined by the animals experience and is subject to change in a short period of observation.

1.7.1.5.5 Categorization of optical systems of eyes

It is recognized that there are a nearly infinite variety of eyes in the animal kingdom. Many are the result of unique adaptations to satisfy the requirements of individual environmental niches. However, based on the above material in this Section, defining a series of precise labels describing the baseline configurations of the different animal eyes is instructive. Although not always shown in various sketches, every eye will be defined by a *camera* containing a single aperture for light gathering purposes. Since eyes are fundamentally change detection devices, having the camera entirely opaque is not always necessary. It is only necessary that it prevent undesired image forming light of a specific wavelength from reaching the photoreceptors sensitive to that wavelength. The combination of the sclera and choroid of the human eye is not opaque in the sense used in photography. In that field, a higher degree of opaqueness is required because the recording material integrates the incident light over a very long time.

If the eye consists of a camera with only a single two-lens group in the aperture and the photosensitive material replicated into an array (retina) some distance from the lens group, the resulting eye is a complex eye. This complex eye is found in two fundamental forms. If the illumination passing through the aperture falls directly on the photosensitive surface of the retina, it is called a direct complex eye. If the illumination passing through the aperture

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[195]Pirenne, M. (1967) Vision and the Eye. London: Chapman & Hall. pg. 20

must pass through the neural material associated with the retina before reaching the photosensitive surface, it is called a reverse complex eye.

All eyes will be considered variants of one of the above types of eyes. As examples, the eye of *Nautilus* is considered an immature form of a direct complex eye. In this case, the lens group has not formed or is currently represented by relatively fluid mucous material. The eye of the male *Xenos, peckii*, a tiny parasite that lives inside paper wasps, is a variant of the compound eye[196]. It employs fewer anterior lenses, about 50, than the normal compound eye and more rhabdoms behind each lens. Each mini-retina is said to contain 100 individual photoreceptors instead of the normal 5-9.

Earlier, **[Figure 1.2.1-6]** summarized the precise names used from now on in this work to categorize eyes. The terms vary slightly from the literature to gain consistency and to recognize certain facts.

Planaria, and the other simplest bilateral animals are generally transparent. They frequently exhibit two rows of photosensitive cells. There is frequently a pigmented ridge near this row of cells that provide a “light stop” that aids in determining the direction of incident radiation. This radiation may arrive directly at the photosensors from outside the animal or it may arrive in the inverse direction by passing through the animal. This configuration is not considered an eye in this work because the photosensing elements are not enclosed by a structure having only one aperture.

The fundamental unit eye, the ommatidium, used in Arthropoda is shown in frame A. This package contains all of the required elements to form an eye. It contains a group of photosensors, generally called a rhabdom. A single rhabdom is frequently described as a retinula, or fundamental unit of a retina. The rhabdom is mounted inside a camera consisting of pigmented material surrounding the rhabdom and the liquid-crystalline material labeled the gel cone. The aperture of the camera is occupied by a lens group in analogy to the other eyes to be discussed below. The prominence of the lens labeled L1 depends on the environment of the animal. It is frequently described in the literature as a cornea or a hard cover. The material between the cornea and lens L2 and between lens L2 and the rhabdom is viscous but not crystalline. It is properly described as liquid-crystalline. It can be compared with the anterior humor and the vitreous humor of the chordate eye respectively.

> The general plan for the optical system of all eyes includes two refractive lenses. The specific properties of these two lenses are varied significantly to provide the great variation in optical performance required to adapt to the local environment of the animal.

Frame B shows one of the evolutionary paths from the ommatidium. The ocellus, or simple eye has the basic form shown although it can appear in a variety of similar configurations. It consists of one large rhabdom containing many individual photosensors. In the case shown, each photosensor is located behind its own second lens, L2, but shares lens L1 with all of the other photosensors within the ocellus. Each Photosensor consists of a single package of chromophore (the horizontal ellipses) associated with individual rhabdomin or photoreceptor cells. The axons of these photoreceptor cells generally connect directly to the brain of the animal. There are no reports of ommatidium or other simple eyes relying upon indirect illumination.

Frame C shows the compound eye of *Arthropoda*. It consists of a replication of the fundamental unit, the ommatidium. The term retinula is replaced by retina in this situation. The retina consists of multiple rhabdoms that are relatively widely spaced because of the size of the individual lens groups compared with the photosensors. There is considerable discussion in the literature concerning the conditions existing between the individual ommatidia. Many of these discussions center on whether there are opaque pigments optically separating the gel cones. These discussions will not be pursued here. There is one important point to make. If the gel cones are in fact light pipes, it is not the absorption of any surrounding pigment that is controlling. The controlling factor is the difference in index of refraction between the interior of the gel cone and the surrounding material. If the difference in index of refraction causes total reflection at this surface, it is immaterial whether the external material is opaque or transparent.

The eyes of *Arthropoda* are generally replications of the fundamental ommatidium, e.g., the complete sensory package including the lens group. These eyes are called compound eyes. The eyes of *Mollusca* and *Chordata* have evolved in a different direction. They have involved the replication of only the photosensor assemblies to form a retina and the separate morphogenesis of a single camera to enclose the entire retina. These eyes are called complex eyes. Mollusca has followed this complex approach to an eye while using direct illumination. Chordata, on the other hand has developed such a complex eye based on indirect illumination. Instead of discussing the eye from the

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[196]Buschbeck, E. Ehmer, B. & Hoy, R. (1999) Chunk Versus Point Sampling: Visual Imaging in a Small Insect Science, Nov. 5, pg. 1178-1180

perspective of indirect, or inverse, illumination, it is generally described as using a reverse retina.

Frame D shows the fundamental eye of *Mollusca* in its typical body-mounted configuration. The similarity to the eye of *Chordata* is obvious. It lacks only the freedom to rotate provided by the eyeball of *Chordata*. The neural portion of the retina of Mollusca is quite simple and there are direct neural paths from most photoreceptors to the brain of the animal. This number of neurons prevents any significant flexibility between the eye and the body of the animal. Mollusca has not developed an iris and, as a rule, has developed only one eyelid capable of covering the aperture of the lens system. To perform the function of the iris, the eyelids of *Mollusca* are much more complex in their shape and operation than the simple shutters used in *Chordata*.

Frame E shows the fundamental eye of *Chordata* except for the frequently present second eyelid. This eyelid is discussed in **Section 2.4.3.3**. The retina is of the reversed type and the entire camera can rotate in two dimensions over a considerable angle. The neural material associated with the retina is much more highly developed than in *Mollusca*. It provides a major signal processing function to reduce the number of nerves that must be included in the optic nerve connecting the highly mobile eyeball to the brain.

Based on this structure, comparing the names given with the various parts of the eyes by different investigators working with different eyes is possible.

Element	*Chordata*	*Arthropoda*	*Mollusca*	Recommended
L1	Cornea	unnamed layer		cornea
	aqueous humor	unnamed volume		aqueous humor
L2	lens, crystalline	cuticular lens		lens, crystalline
	vitreous humor	crystalline cone (l. pipe)		vitreous humor
L3	field lens	- -		Field lens

The field lens is only known to appear in Anthropoids of *Chordata.*

1.7.2 Generic Retinal Systems

The number of block diagrams and simple schematics of the retina found in the literature is overwhelming. However, most of them are conceptual models based on psychophysical data. Until the work of Svaetichin and Tomita in the 1950's, they lacked any significant electrophysical foundation. Since then, they have been hampered by the desire to comply with concepts dating from the 1920-30's, and earlier. These concepts have relied upon three synthetic spectral characteristics known as the tristimulus values of the C.I.E (also known as the color matching functions of the R, G, B or X, Y, Z systems). They have also been influenced significantly by the cross section of the retina presented by Polyak in 1941.

One of the more recent of these block diagrams is that of Ratliff[197]. The diagram suffers from a variety of problems. They begin with his choice of spectral peaks in the absorption spectra of the three chromophores of the trichromat. These are based on the conventional wisdom instead of hard experimental results. It also appears to adopt a Hering approach to signal processing and arbitrarily to place the role of adaptation after the role of lateral summation. In this work, it will be shown that the sequence of events is different. The system is best described as performing photodetection, transduction, adaptation (in that order) and then introducing a division of the signal paths into three channels unrelated to individual spectrums. These channels include a luminance channel, involving logarithmic summation, and two chrominance channels involving logarithmic subtraction. Whereas Ratliff used the terms differentiation and compression in his model, the words were not adequately defined to discuss them further in this introduction. A more precise block diagram is presented in **Chapter 11.**

Three basic designs for the organization of the photoreceptors of vision are found in animals. The one usually thought of is that used by the animals of *Chordata*[198] (which includes all of the vertebrates). The eyes in the phyla *Mollusca* and *Arthropoda* (which includes the insects, spiders etc.) are the other organizations. All these eyes have evolved from the simple photo spot of the ancient worms such as planaria. The eyes of *Arthropoda* consist of the "simple eye," consisting of a single cartridge of photoreceptors behind a single optical assembly, and the compound eye that essentially consists of an aggregate of these simple eyes.

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[197]Ratliff, F. (1976) On the psychophysical basis of universal color terms. Proc. Am. Phyl. Soc. vol. 120, pp. 311-330

[198]Hickman, C. (1970) Integrated principles of zoology. 4th Ed. St. Louis MO: C. V. Mosby pg 126

Arthropod and mollusc eyes have evolved without the requirement to provide rapid eye rotation and therefore have a simpler form with the neural connections not in the visual pathway (the directly illuminated retina). Chordate eyes have evolved with what could be considered an awkward form, some neural tissue inserted in the optical pathway ahead of the photoreceptors (the indirectly illuminated retina). As discussed below, this form has its positive and negative aspects.

Earlier, **[Figure 1.2.1.7]** showed a variety of retinal formats based on geometry. The generic retina consists of multiple units of a cluster containing multiple photoreceptor cells sensitive to up to four separate spectral regions. Sometimes, pairs of photoreceptor cells are provided to sense one spectral band in two orthogonal polarizations. The clusters are generally closely packed except in the simple and compound eye of *Arthropoda* where the optical system determines the density of the clusters of detectors. As seen in the chordate retina, the packing can frequently be described as rectangular or hexagonal based on the whim of the author.

Polarization sensitivity of one degree or another has been documented in more than 100 animals in all phyla[199]. It is the norm in *Arthropoda*, common in *Mollusca* and less frequent in *Chordata*.

In discussing the organization of different retinas, it is useful to keep in mind the potential for twelve different photochemical architectures involving the four spectral regions and the three types of Vitamin A used to create the chromophores of vision. Neglecting polarization and noting that a given species within a phylum need not use all of the chromophores commonly found in that phylum, a sparse three by three matrix can be constructed describing the currently known situations. A researcher on the leading edge of determining the architecture used in a specific family of animals can correlate his data against this matrix. The three by- matrix includes:

+ tetrachromatic vision utilizing *four* distinct chromophoric channels; UV, S, M & L
+ Trichromatic vision using the upper three distinct chromophoric channels; UV, S & M
+ Trichromatic vision using the lower three distinct chromophoric channels; S, M & L

The by-three matrix includes:

+ The chromophoric set based on the chromogen Vitamin A_1, retinol
+ The chromophoric set based on the chromogen Vitamin A_2, $retinol_2$
+ The chromophoric set based on the chromogen Vitamin A_3, $retinol_3$

Table 1.7.2-1 summarizes this matrix and shows a few examples. The examples are only indicative because the species within a family may have evolved into an environment where the use of a different form of Vitamin A is better.

TABLE 1.7.2-1
RETINAL SYSTEMS BASED ON THE TYPE OF VITAMIN A CHROMOGEN

Type of Vitamin A	Vitamin A1	Vitamin A2	Vitamin A3
Spectral Group		Family or Species	
Short wave triad	insects		? Diptera
tetrad	mammals	Small Rodents	? Diptera
	Birds		
	Reptiles	Reptiles	
	Small Fish		
long wave triad	Freshwater Fish	Marine Fish	
		Most Terrestrial	? Some Rodents

[199]Waterman, T. (1975) Op. Cit.

This matrix is further complicated by two additional considerations. The diadromous animals, primarily fish, change their baseline relative to Vitamin A during their lifetime as they migrate from salt water to fresh water. There are also a variety of animals which use a tetrachromatic configuration, but only during a part of their lifetime. The changes in the diadromous animals do not involve a significant change in peak spectral absorption for the individual chromophores. The peaks remain orbiting very close to the nominal values of 342, 437, 532 & 625 nm. The peaks may change more due to temperature than to the source of Vitamin A.

1.7.2.1 *Arthropoda*

The ommatidia of both the simple and compound eye will be considered together in this section as there is little documentation showing them to be different.

1.7.2.1.1 Multi-spectral ommatidia

Many authors have provided individual cartoons of the various rhabdoms found within an ommatidia of arthropod eyes. Menzel & Backhaus have provided a composite of some of these different configurations[200]. Tomlinson has also provided a good review focusing on *Drosophila*[201]. Other sources include Wu, et. al[202]. and Feiler, et. al[203]. It is necessary to say these papers do not include any model of the system they are attempting to define.

The intent in **Figure 1.7.2-1,** from Menzel & Backhaus, is to show a single rhabdom of the fly, bee and moth in the same context. The caption for the original figure consumes most of a whole page. As seen in the figure, the terminology remains conflicting between different investigators. The three small insets along the side of the main sketches are meant to be equivalent structures. However, they are not drawn from the same conceptual perspective. In the case of the fly, the rhabdomeres are shown as small filled circles withing the rhabdom and the cell walls separating the photoreceptor cells are not shown at all. In the bee and the moth, the cell walls separating the individual photoreceptors are shown but the rhabdomeres associated with each photoreceptor cell are not shown at all. Similarly, the sketches along the bottom row appear meant to be similar. However, they also are not. The lower left sketch shows a group of seven individual rhadoms in an array, not the one rhabdom as implied by the label. For the bee and the moth, the large dark area is meant to represent the fused rhabdomeres of the individual photoreceptor cells. The cell walls between the photoreceptor cells have been omitted in these two caricatures and a hexagon has been drawn around the circle representing the exterior of the group of cells in the upper sketches. In the lower left sketch, the individual rhabdomere are shown separately, giving the name to the structure, the open rhabdom. The circle representing the circumference of the group of cells has been omitted in this sketch.

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[200]Menzel, R & Backhaus, W. (1991) Color vision in insects. *In* The Perception of Color, Gouras, P. *ed*. Boca Raton FL: CRC Press pp. 264

[201]Tomlinson, A. (1988) Cellular interactions in the developing *Drosophila* eye. *Development*, vol. 104, pp 183-193

[202]Wu, Louisa. et. al. (1995) Regulation of PLC-mediated signalling *in vivo* by CDP-diacylglycerol synthase. Nature, vol. 373, pp 216-222

[203]Feiler, R. et. al. (1992) Ectopic expression of ultraviolet-rhodopsins in the blue photoreceptor cells of Drosophila . . . *J. Neurosci*. vol. 12(10) pp 3862-3868

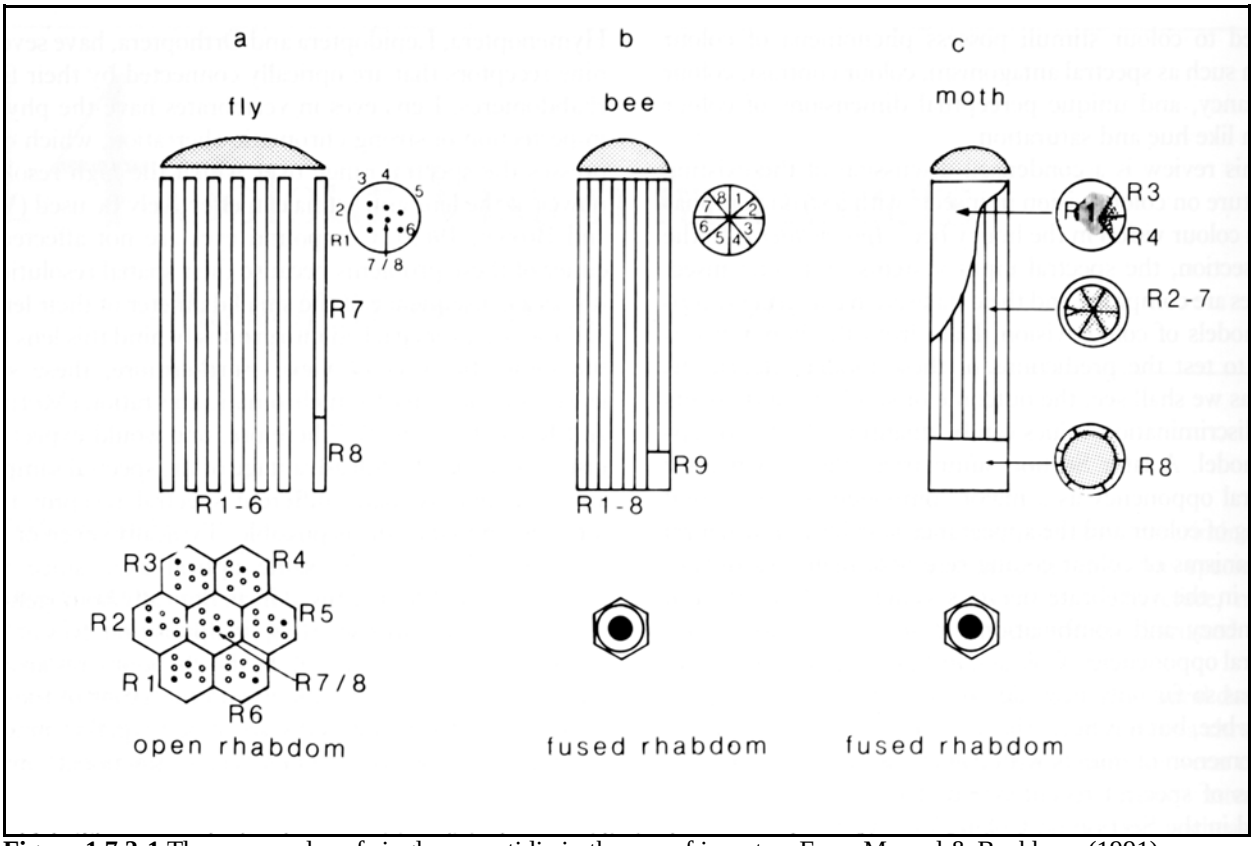

Figure 1.7.2-1 Three examples of single ommatidia in the eye of insects. From Menzel & Backhaus (1991)

An additional significant complication related to this figure is the fundamental architecture of the ommatidia. This fundamental architecture typically consists of a group of seven photoreceptor cells viewable from the proximal end of the ommatidia. An eighth cell is usually present. It is not normally visible from the proximal end of the rhabdom. It may or may not be photosensitive. It may or may not act as a signal manipulation neuron. In many species, this cell is not photosensitive and acts as a multi-input bipolar neuron. In the primitive *Limulus*, a member of *Arthropoda*, the cell can be considered a multi-input bipolar neuron, but is better described as a ganglion cell. It accepts electrotonic signals at its input and produces pulse signals (action potentials) at its output.

The photoreceptors of a single ommatidia exhibit different spectral characteristics and are frequently arranged in pairs. The pairs are frequently on opposite sides of the ommatidia. No physical difference in the morphology of the photoreceptor cells has been proposed based on spectral performance (such as that frequently proclaimed for photoreceptors in the eyes of *Chordata*). Menzel & Backhaus provide a histogram of the spectral performance of the photoreceptors in various insect eyes. They show these peaks to be grouped around 336, 432 and 532 nm with a small group of insects exhibiting an additional peak at 625 nm. These are the precise spectral peaks, within plus or minus three nanometers, predicted on theoretical grounds by this work. Unfortunately, they use a different nomenclature to describe the visual channels. They (and others) use the designations S-, M-, L-, & VL- (the last being very long), when discussing *Arthropoda*, instead of the series UV-, S-, M-, & L- (the first being ultraviolet) used in most chordate oriented work. Care must be taken in reading the literature to differentiate between an S-channel in *Arthropoda* (max sensitivity near 342 nm) and an S-channel in *Chordata* (max. sensitivity near 437 nm). The same problem is found with the M- and L- channel designation. Using the designations UV-, S-, M-, & L- exclusively avoids this problem.

Kitamoto, Ozaki & Arikawa have recently provided good tetrachromatic data on the butterfly, *Papilio xuthus*[204].

[204]Kitamotom, J. Ozaki, K. & Arikawa, K. (2000) Ultraviolet and violet receptors express identical mRNA encoding an ultraviolet-absorbing opsin. . . . *J. Exp. Biol*. pp 2887-2894

They have used the conventional notation of UV, S, M & L to explain the tetrachromatic performance of vision in this arthropod. They also provided a useful bibliography.

Still more recently Chen, Awata, Matsushita, Yang & Arikawa have provided a more complex cartoon related to the butterfly ommatidium[205]. The cartoon was discussed briefly in **Section 1.2.1** and will be discussed further in **Section 3.6.** Their paper is extensive but does not provide any block diagram or schematic of the butterfly eye except for a relatively simple cartoon. Their figure 1 is presented as **Figure 1.7.2-2**. The unlabeled central hatched column represents the active absorption column of ommatidia, the rhabdom.

They indicated the presence of a selection of fluorescing pigments; a UV fluorescing pigment near the top of the ommatidium and a reddish pigment below the letters C, C' in the figure. Both pigments surround the active receptor area defined by the central column, the rhabdom. These pigments may complicate their experimental protocol and results in their discussion. Whether these pigments are excited within the natural environment was not discussed in the paper. Based on closer evaluation of their electron-micrographs, it does not appear these pigments play a role in active photoreception. These pigments appear to be stored in cells equivalent to the RPE of the chordate eye and distinctly removed from the matrix surrounding the rhabdom. They distinguish between their dorsal and ventral ommatidia within the compound eye.

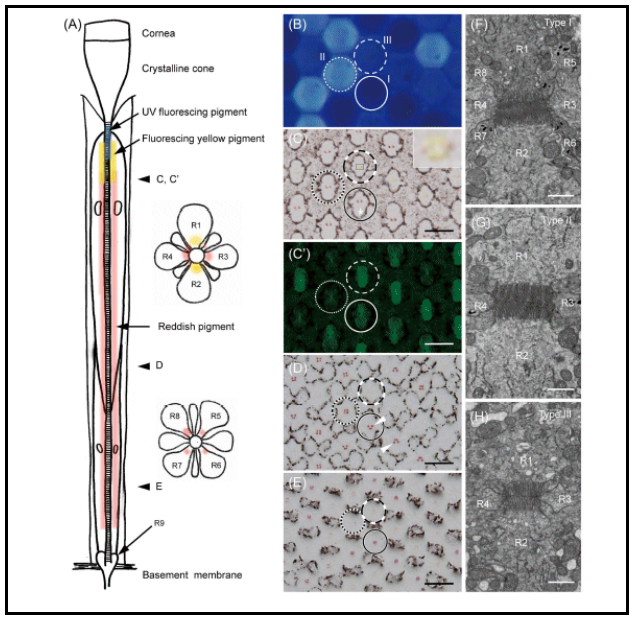

Figure 1.7.2-2 The ommatidia of Graphium Sarpedon ADD. The panels on the right are shown for completeness but are not discussed in this work. Two distinct sets of photoreceptors are shown, possibly due to different stages of adaptation. Receptor R9 is shown near the basal membrane. See text. From Chen et al., 2016.

1.7.2.1.2 Polarization sensitive retinula

An exception to the placing of the photoreceptor cells of similar spectral performance on opposite sides of the ommatidia frequently occurs. When the goal is to achieve a sensitivity to polarization within a single spectral band, the pair of cells are placed so that their rhabdomere can be arranged orthogonally to each other and to the direction of the incoming radiation.

Waterman[206] has provided a detailed sketch of the polarization sensitive rhabdom (retinula) of a crustacean as he saw it. It shows a rhabdom similar to the typical arthropod rhabdom except for the elimination of any rhabdomere located in the axial position. Instead, the remaining rhabdomeres are shown interdigitated. The letters and numbers have been added to **Figure 1.7.2-3** for discussion. The notation is slightly different from that of Waterman[207]. It is not obvious why the rhabdomin at **A** should be larger than the others and be opposed by two separate rhabdomin. It is possible this is atypical. If **A** is actually two rhabdomin, i.e., **7** & **8**, the rhabdom would be able to sense polarization in up to four different spectral regions. If **A** is as shown, the animal could still sense polarization in at least three spectral bands using **2** & **3**, **4** & **5**, and either **6** & **A** or **1** & **A**. Without more knowledge of the spectral sensitivity of the different rhabdomeres, little more can be said. Any computation involving the processing of signals from these rhabdoms would depend on the chromatic sensitivity of the individual photoreceptors. Many arthropods are sensitive to the amplitude of illumination in four separate spectral regions; no record was found showing any are sensitive to polarization in all four regions. The common wisdom suggests that polarization sensitivity in the ultraviolet would be most beneficial in navigation.

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[205]Chen, P-J. Awata, H. Matsushita, A. Yang, E-C. & Arikawa, K. (2016) Extreme Spectral Richness in the Eye of the Common Bluebottle Butterfly, Graphium sarpedon *Front Ecol Evol* vol 4, article 18 | http://dx.doi.org/10.3389/fevo.2016.00018

[206]Waterman, T. Fernandez, H. & Goldsmith, T. (1969) Dichroism of photosensitive pigment in rhabdoms of the crayfish *Orconectes*. J. Gen. Physiol. vol. 54, pp 415-432

[207]Waterman, T. (1975) Natural polarized light and *e*-vector discrimination by vertebrates. *In* Evans, G. Bainbridge, R. & Rackham, O. *ed*. Light as an ecological factor: II Oxford: Blackwell Scientific Publications, Chapter 13, pp 305-

Snyder & Pask has extended the analysis of polarization to note the need to align the various groups of microvilli with the optical modes of the light that can be supported within the waveguide-like structure of the rhabdomere[208]. This study surfaces the possible reasons for some rhabdomere to be arranged with their individual spectral absorbers located around the periphery while others appear to be interdigitated.

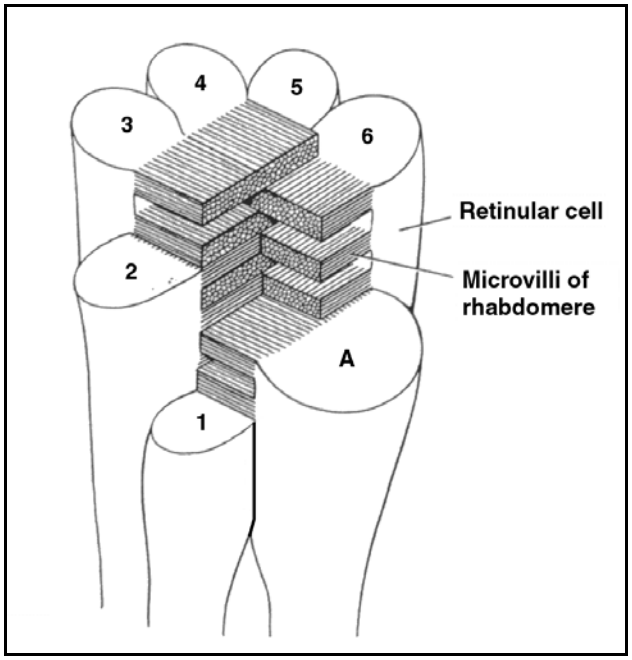

Figure 1.7.2-3 The polarized-light detector of the crustacean eye showing the interdigitating of rhabdomere consisting of groups of rod-like structures, within the central rhabdomin. The large volumes of the soma of individual sensory receptors (numbered and lettered) are not light sensitive. From Horridge, 1968.

1.7.2.1.3 Polarization sensitivity via stereopsis

Dacke, et. al[209]. have reported a possible variant on the basic polarization capability of *Arthropoda*. They found that the two skyward facing eyes of *Drassodes cupreus*, a spider believed to be native to Sweden, are oval with their major axes perpendicular to each other. The eyes exhibited absorption peaks at 350 (342) nm and 500 (532) nm. The values in parentheses are the predicted peak values based on this work. The value at 500 nm could be the result of a Brezold-Brucke Peak at 494 nm. These values will be discussed extensively later. The investigators suggest that the eyes work as a pair to detect polarization of the solar illumination primarily at early and late times of daylight. The inference being that the signals from the two eyes must be compared in a structure similar to the LGN of chordates. They found no sign of polarization by the dioptric optical system. They did find indications of polarization due to both the tapetum acting as a mirror and the intrinsic structure of the photoreceptor cells.

Their introduction suggests both insects and vertebrates can detect the polarization of light. However, they did not discuss the ability of *Mollusca* in this regard.

1.7.2.1.4 The complicated eye of the Mantis Shrimp

The crustaceans are a group that is difficult to place within the phylogenic tree, partly because of their great diversity of visual systems. Cronin, et. al. have provided references and data on a stomatopod crustacean, colloquially known as the mantis shrimp[210]. Technically, it is neither a mantis nor a shrimp. It is characterized by what they describe as a "triple compound eye." The complexity of its visual system is so great it must be referenced here. Particularly good data on polarization sensitivity in the ultraviolet (345 nm) is provided. They describe the polarization sensitivity to be maximum when the *e*-vector of the light is parallel to the length of the microvilli. Snyder & Menzel address the subject of *e*-vector orientation from a general perspective[211].

During the 1990's, a team led by Marshall has provided an abundance of information on the eyes of the mantis shrimp[212,213]. Some of their press releases and short communications have led to confusion. They variously claim from 8 to 11 spectral classes of photoreceptors in this species. The authors were careful to state their position in the last paragraph of their summary (page 81), "It is the photostable filtering and screening pigments, rather than the

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[208]Snyder, A. & Pask, C. (1972) Light absorption in the bee photoreceptor. *J. Opt. Soc. Am.* vol. 62, no. 8, pp 998-1008

[209]Dacke, M. Nilsson, D. Warrant, E. Blest, A. Land, M. & O'Carroll, D. (1999) Built-in polarizers form part of a compass organ in spiders. Nature, Sept. 30, pp. 470-473

[210]Cronin, T. Marshall, N. Quinn, C. & King, C. (1994) Ultraviolet photoreception in mantis shrimp. *Vision Res.* vol. 34, no. 11, pp 1443-1452

[211]Snyder, A. & Menzel, R. (1975) Photoreceptor optics. NY: Springer-Verlag, pg 5

[212]Cronin, T. & Marshall, N. (1989) Multiple spectral classes of photoreceptors in the retinas of gonodactyloid stomatopod crustaceans *J Comp Physiol A* vol 166, pp 261-275

[213]Marshall, N. Land, M. King, C. & Cronin, T. (1991) The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda) *Phil Trans R Soc Lond B* vol 334, pp 33-84

visual pigments, which are examined in detail in this paper." They then used the term visual pigments in two different contexts. Many of the spectral peaks they report are due to a combination of chromophores, tissue filters in the optical path and post detection signal processing. In fact, there are only four distinct chromophores in *Arthropod* vision, peaking at 342, 437, 532 and 625 nm. However, they are used in a set of configurations that also offer polarization sensitivity as discussed above. The authors note spectral peaks at 315 and 330 nm. These peaks are well documented as due primarily to protein absorption by non-photosensitive tissue (See **Section 2.4.2**–**Figure 2.4.2-4**).

The team did note the presence of carotenoid materials in the photoreceptor cells of the retinulas but did not explore them in detail.

The Marshall team did not record spectra peaks associated with the chromophores because they did not realize the chromophores absorption characteristics were anisotropic. They only recorded the trivial isotropic spectral peak at 503 nm associated with non-conjugate retinal. This absorption peak is not actively used in vision (**Section 5.3.5.3.2**). To record the active peaks associated with the conjugated chromophores, their microspectrophotometer[214] beam must be parallel to the optical axis of the rhabdom.

1.7.2.1.5 The compound eye of the butterfly– work of Arikawa et al.

During the last two decades, Arikawa and colleagues have built on the earlier work of Stavenga and provided extensive information concerning primarily butterflies. See **Section 3.6**. At least three major papers will be addressed in that section. Detection of the polarization of the light received by the eyes of *Insecta* appears to be a much more important role than in *Chordata* and *Mollusca*.

There are cautions that need to be reviewed before analyzing these papers.

1. It is important to distinguish between a pigment (in bulk form and generally stored separately from a rhabdom) from an active chromophore (present in liquid crystalline form deposited on a microvilli, or in the case of chordate eyes on the disks of the outer segment. These forms can exhibit significantly different spectra even though they consist of the same chemical molecule. A pigment denotes a material that is observed visually by reflected light whereas a chromophore is a material that absorbs light passed through it. The color of a chromophore resulting from observing the color that passes through it is the complement of its absorption spectrum (**Section 17.3.4.3**).

2. When in the liquid crystalline form, the chromophores may exhibit anisotropic absorption spectra. Generally, the spectrum used in vision is the narrow band spectrum with high sensitivity when excited by light traveling parallel to the axis of the conjugated atoms within the molecule.

3. Most "color" recording media, such as photographic film and conventional television equipment will not sense and cannot present information present in the samples under examination. As a result, a pigment (observed by reflected light) related to a UV chromophore may appear to reflect little light over a broad spectrum. When observed using the above equipment by transmitted light (sometimes described as back-lighted), the UV chromophore may appear to be transparent. The granules present in the RPE of chordates are examples (**Sections 4.5** & **4.6.2.2.3**). In [**Figure 4.5.1-1**], the chromophores are described by their absorption spectra. [**Figure 4.6.2-6**] shows actual imagery of the RPE by transmitted light from Wolken, 1966.

4. The labels used by the Arikawa investigators (and many others) do not recognize the difference between the names of colors observed by reflected light and those observed by transmitted light. The labels are frequently significantly different from those adopted by the US National Bureau of Standards and the CIE (**Section 2.1**) While the difference between purple and magenta may appear semantically trivial, purple is the name of a spectral color (generally at 410 nm and observed by transmission), while magenta is a non-spectral color (consisting of a mixture of red, ~625 nm, and blue, 470 nm) observed by reflection. Magenta is frequently labeled 532c nm, the complement of the peak of the M – channel chromophore at 532 nm.

The distinction between purple and magenta is not observed in the papers cited in this section. Neither is the distinction between yellow (570 nm) of the CIE and the yellow of these papers (520 nm).

5. "Lucifer yellow CH, lithium salt is a water-soluble dye with excitation/emission peaks of 428/536 nm. It is a favorite tool for studying neuronal morphology, because it contains a carbohydrazide (CH) group that

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[214]Cronin, T. (1985) The visual pigment of a stomatopod crustacean, Squilla empusa *J Comp Physiol A* vol 156, pp 679-687

allows it to be covalently linked to surrounding biomolecules during aldehyde fixation" according to Thermo-Fisher Scientific. They note this material is "For Research Use Only. Not for use in diagnostic procedures." The 428 nm emission line is poorly observed by the human eye and poorly recorded by most photographic and TV equipment. The emission at 536 nm is more yellowish–green (where yellowish is an adjective modifying the noun green) than yellow using the NBS and CIE nomenclature. A much better yellow "pigment" is strontium chromate, $SrCrO_4$ with a peak reflectance at 572.3 nm . The visual modality of *chordata* does not use any chromophore absorbing near 570 nm. Yellow is a perceived color based on computation within the central nervous system (CNS), **Section 17.3.4.2**.

6. The use of pigment will continue to be used in both situations in **Section 3.6** to avoid confusion between quotations from the literature and assertions related to that literature in this work.

Many of the above cautions apply to the discussions of the eyes of Mollusca as well (See **Sections 1.7.2.2** and **3.5**.

1.7.2.1.5 The chromatic aspects of bee eyes–Vasas & associates

Vasas[215] et al. provided an expansive article on the potential signal processing in the eyes of bee. The paper includes excellent data but lacks any null hypothesis concerning the physiology of the visual modality of the bee. The do identify the three chromatic channels of the system with peak sensitivities at ≈344 nm in the UV, ≈436 nm in the blue and ≈544 nm in the green. Unfortunately, they label the UV channel as S–, the channel peaking at 436 nm as —- and the channel peaking at 544 nm as L–. Their set 344, 436, 544 compares very favorably with the set for animals at 342, 435, 532 and 625.

They note; "*A simple model can reproduce previously measured spectral response curves with one morphological neuron type*." This is consistent with this work where all photoreceptors are morphologically identical with only their selection of chromophores varying.

Their figure 2 appears to identify both the primary spectral channels but also a "Magenta-like" spectra summing the 342 nm and 532 nm channels. They also identify a signal that appears to be an inversion of the UV channel minus the blue channel with a peak near 395-400 nm.

They do base their analyses on a quantum-catch assumption rather than an energy-catch assumption. But then they make the assumption that all combinations of signals from their three channels are randomly wired to generate a potential of 26 different spectral channels.

They note; "*This diversity is at odds with the notion that colour-coding neurons in bees are wired deterministically*." However, their figure 1 closely resembles, and uses familiar names for neurons of their medulla, the stage 2 signal processing within the animal (*chordata*) retina. Their figure 1 is more than adequate for hypothesizing a stage 2 signal processing virtually identical to the animal system defined in this work (Chapter 13). They assert in the caption of that figure, "*The model presented in this paper analyses in detail the spectral profiles of third-order colour sensitive neurons.*" They then proceed to assert, "*Most importantly, the morphology assumed for all third-order cells is the same. . . but each cell is characterized by a different response threshold and different, randomly distributed presynaptic input weights.*"

The italicization added above strongly suggests their third order cells are the equivalent of the ganglion cells of the chordate retina (although they do not generate action potential because of the short distances within the visual modality of bees). The ganglion neurons have input mappings very similar to that described by Vasas et al.

The data in the paper strongly suggests an organization of the visual modality of Insecta virtually identical to that of Chordata, except for the lack of a long wavelength channel with peak sensitivity near 625 nm.

Their Discussion is quite interesting but does not limit the neural circuitry to a random process versus a deterministic process. Note the use of the term "*might*" in the lead sentence of their last paragraph, "In conclusion, our study adds to the growing body of data indicating randomness might be an important organizing principle in vision."

1.7.2.2 *Mollusca*

[215]Vasas, V. Peng, F. MaBouDi, H. & Chittka, L. (2019) Randomly weighted receptor inputs can explain the large diversity of colour-coding neurons in the bee visual system *Sci Reports* vol 9, article 8330 https://doi.org/10.1038/s41598-019-44375-0

Messenger reviewed the available data in 1991[216] and noted the immense morphological diversity in the photosensitive elements in the phylum. This varies from a variety of simple photosensitive cells, through simple eyes, to the highly-developed complex eyes of the cephalopods.

1.7.2.2.1 Multispectral mollusc retina

As a phylum, it contains all of the expected chromophoric spectral bands. The literature specifically reports the presence of the UV-, S-, & M-channels as expected due to anisotropic absorption by the rhabdom. It also reports a frequently recorded isotropic peak at 500 nm. The instrumentation used to measure this peak must be examined in each case. The arrangement of the chromophoric material in the retina of the higher *Mollusca* seems to facilitate the measurement of an isotropic (nonfunctional) peak at 500 nm.

Limited detailed information is available on the retina of the more advanced members of *Mollusca*. It obviously consists of multiple individual photoreceptor cells in a two-dimensional array lining the inside of an enclosure opposite the aperture. The retina is of the direct type. The photoreceptors are illuminated at their distal end. The cartoons of Eaken, Wolken and others are relatively simple and difficult to correlate to a two-dimensional array. Both spectral and behavioral data show that the retina is sensitive to at least the S- and M-chromophores[217]. The spectral response recorded by Hamasaki,[218] using electroretinographic techniques, also suggests sensitivity in the ultraviolet spectrum. The animal is sensitive to the polarization of light in at least one spectral region. Young has provided the most details on a retina of *Mollusca*[219] in **Figure 1.7.2-4.** This hand drawn caricature is apparently based on visual microscopy. Many finer details expected from an electron micrograph are missing. The identification of the views is also questionable from a draftsman's perspective. The lower view was not originally aligned to the upper view. It has been realigned in this figure. The lower view appears to be a side view along a fractured surface rather than a true section view. The supporting cells are not as prominent in the upper view as in the lower view. The abbreviations are: *bas*., basement, *ce*., cell, *co.*, collateral, *eff*., efferent, *ep*., epithelium, *f*., fiber, *in*., inner, *lim*., limiting, *mem*., membrane, *nuc*., nucleus, *out*., outer, *pig*., pigment, *pl*., plexus, *ret*., retina, *rh*., rhabdom of retina, and *su*., supporting.

There are two important aspects of the tangential section. First, the individual cells In the tangential section are seen to be symmetrical with the retinula in the center and rhabdomere extending from opposite sides. The heavy black lines, representing four adjacent rhabdomins, appear to form a box like unit similar to that of the crustacean eye. This group could

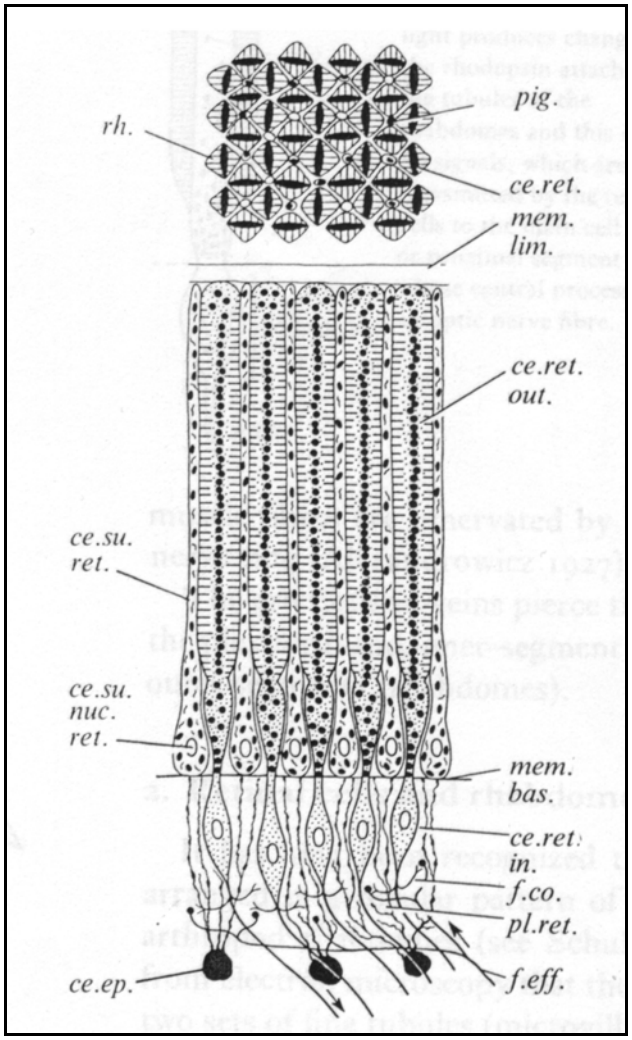

Figure 1.7.2-4 Diagram of the retina of *Octopus*; above as seen in tangential section and below in radial section. See text for interpretation and abbreviations From Young (1971)

[216]Messenger, J. (1991) Photoreception and vision in Molluscs. *In* Evolution of the eye and visual system. Cronly-Dillon, J. & Gregory, R. *ed.* Vol. 2 of Vision and Visual Dysfunction. Boca Raton, FL: CRC Press, pp. 364-397

[217]Cronly-Dillon, J. (1966) Spectral sensitivity of the scallop *Pecten maximus*, Science, vol. 151, pg. 345-346

[218]Hamasaki, D. (1968) The electroretinogram of the intact anaesthetized octopus. Vision Res. Vol. 8, pp. 247-258

[219]Young, J. (1971) The anatomy of the nervous system of Octopus Vulgaris London: Oxford University Press Chap. 16

be called a rhabdom if one ignores the rhabdomere extending outward from the cells into adjacent rhabdoms. On the other hand, a diamond shaped rhabdom can be defined by four rhabdomin arranged in a cross. This rhabdom consists of four complete rhabdomins, including both rhabdomere of each cell. This assumes the rhabdomeres are not interdigitated. Assuming this latter arrangement forms a rhabdom, it is interesting to note the presence of two pairs of cells arranged similarly to that of the crustacean eye shown in the previous figure. The caricature of *Octopus* does not show the interdigitating of rhabdomere although higher resolution work might. It does show rhabdomere arranged orthogonally which is usually associated with sensitivity to light polarization. If this assumption is correct, each rhabdom would include two pairs of rhabdomins. It is quite possible that one pair incorporates the S- and one pair the M- chromophore. The result is an individual rhabdom that is both polarization and color sensitive at two wavelengths. If this interpretation is reasonable, the locations at the center of the rhabdomeres of a given rhabdom, and marked *pig*. in the upper figure, would be the equivalent of the IPM of the chordate eye. An inset has been added to the figure focusing on the proposed unit rhabdom. It is consistent with one of the supporting cells providing structural support to, and with pigment material placed around the periphery of, each of these groups. The material surrounding each of these rhabdoms could also act as the wall of a light pipe. Saibil & Hewat[220] have provided an alternate configuration and excellent electron micrographs. It shows the OS of the retinula to be 200-300 microns long with the orthogonal microvilli (coated dendrites) about one micron long and 60 nm in diameter. The diameter is consistent with the diameter of the microtubules along the disk stack in *Chordata* and with the dimensions required to form a distributed Activa. Their characterization of the detailed microvilli arrangement is based on a single retinula and varies slightly from the above interpretation because of their attempt to maintain a cell configuration similar to the Young template for *Chordata*.

Second, the orientation of this figure is unknown with respect to the axis of symmetry found in the *Octopus* eye. As shown above, the Octopus retina exhibits an axis of symmetry formed by the projection onto the retina of the plane formed by the pivotal axis of the eye and the center of its aperture. The angle between the retinal array and the axis of symmetry could be important when discussing the effect of tremor on the performance of the total visual system.

Valuable insight is also available from the side view of the fractured retina (radial section). The most important feature is that there is essentially no signal processing performed within the retina of *Mollusca*[221]. The axons of the photoreceptor cells go directly to the adjacent optic lobe of the brain. There are no lateral processing and no encoding by projection neurons. The figure shows a few efferent fibers entering the retina and contacting the photoreceptor cells through collateral fibers of unspecified function.

Under the above interpretation, the rhabdom of *Mollusca* is less well defined than the rhabdom in *Arthropoda* but better defined than the rhabdom (if any) in *Chordata*. The output of the photoreceptor cells goes directly to the brain without using projection neurons as in *Chordata*. This is the same configuration as in *Arthropoda*.

1.7.2.2.2 Details of the rhabdom

Having electron microscopy of the Octopus retina would be useful. Lacking that data, **Figure 1.7.2-5** illustrates the basic geometry of a single mollusc photoreceptor based on Young and using his hierarchal notation[222]. Although the Young figure showed the rhabdomere of each cell forming triangular collection surfaces, it is proposed that they are more likely to form rectangular surfaces interdigitated with adjacent photoreceptors both across from and perpendicular to this cell. It is also proposed that the features he labeled as “pig” are the Golgi apparatus or mitochondria. In this interpretation, the chromophoric material would be provided from another cell nearby.

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[220]Saibil, H. & Hewat, E. (1987) Ordered transmembrane and extracellular structure in squid photoreceptor microvilli *J. Cell Biol*. vol. 105, pp 19-28

[221]Young, J. (1971) Op. Cit. Chap 17

[222]Young, J. *1971) Op. Cit. pg 420

It is proposed that: the photoreceptor cell consists of a nucleus placed proximal to the basal membrane of the retina (as shown) but with an Inner Segment located distal to that membrane. The primary purpose of the Inner Segment is to secrete and extrude multiple cilia of the protein material, opsin, in a direction perpendicular to the length of the Inner Segment. These cilia (rods of protein) are similar to those in *Arthropoda* and the equivalent of the disks formed in the eyes of *Chordata*. Upon coating with a liquid crystalline chromophore and contacting by a dendrite of the Inner Segment, these structures become the photosensitive rhabdomere of the cell. The dendrites would be expected to be approximately 250 nm in diameter and can only be identified through electron microscopy. The primary role of the supporting cells of the retina is to produce the chromophoric material and transfer it to the IPM. In this role, they are analogous to the RPE cells of *Chordata*.

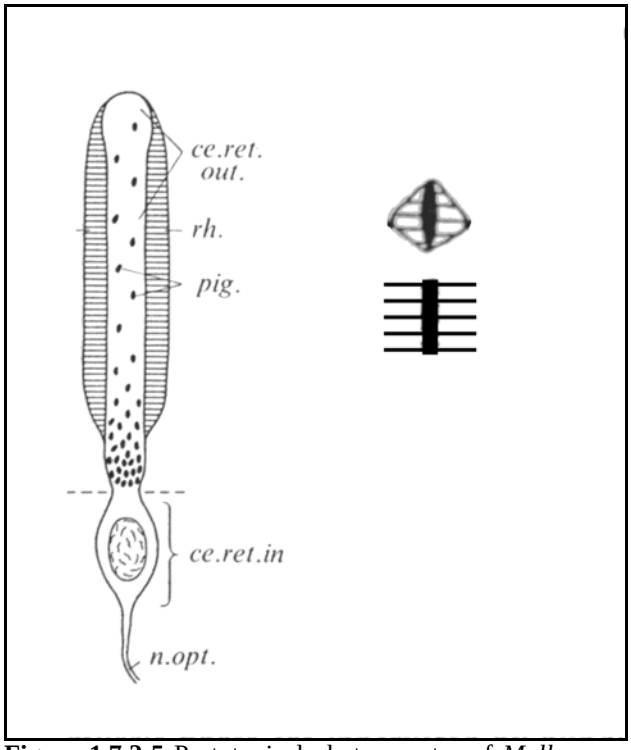

Figure 1.7.2-5 Prototypical photoreceptor of *Mollusca*. The form caricaturized by Young in 1971 is shown on the left and upper right (in cross section). The lower right shows an alternate cross section providing higher sensitivity and polarization sensitivity through inter-digitization.

1.7.2.2.3 The retina of *Pecten maximus*

More data is available, at a gross level, for the unusual case of *Pecten maximus*[223]. **Figure 1.7.2-6** shows that *Pecten* has two separate retina that appear to be arranged back to back. This would imply that one retina must be of the reverse type. However, as seen in the section on mollusc optical systems above, this conclusion is incorrect. Although the two retina are back to back in a physical sense, they are not in the optical path sense. If this cartoon of Land is correct and if the generic eye of *Mollusca* contains a single direct retina, *Pecten* took advantage of an opportunity. It pushed its original retina away from the aperture, and backfilled with a new retina near the argentea. The result is a mollusc with two reverse retinas in each eye. More careful measurements might locate the two focal surfaces differently. This result would be consistent with two direct retinas in each eye. As indicated earlier, the transmission efficiency of this eye is poor because the unfocussed light must pass through one retina before imaging at the proper image surface. A probable 50% of the light is lost in this process.

[223]Land, M. (1965) Image formation by a concave reflector in the eye of the scallop, *Pecten maximus*. J. Physiol. (London) vol. 179, pp. 138-153

The individual photoreceptors are similar in structure to those of Arthropoda, i.e., the chromophoric material is found in rods exuded from the sides of the photoreceptor cells. This similarity leads some authors to use the same element names as in Arthropoda. However, this is not done consistently and confusion is the result. Major differences appear at the next higher level of organization. Whereas the rhabdom of Arthropoda exhibits a circular symmetry with resp10ect to the centerline of the assembly, this is much less evident or nonexistent in Mollusca. The limited data available indicates an orthogonal grouping of photoreceptor cells to achieve a higher sensitivity to the polarization of the incident light.

It is likely that these groupings are repeated across the retina with different groups employing different chromophores to achieve spectral diversity. As indicated in the figure, it is possible that a single group of orthogonal cells could employ more than one chromophore. Further research will be needed to learn the true organization of the retina.

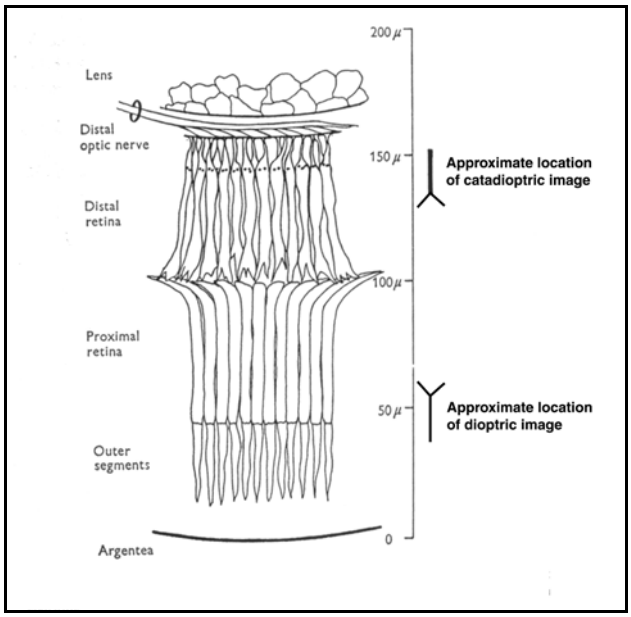

Figure 1.7.2-6 Structure of the dual retina of *Pecten maximus* and the location of the two focal surfaces. The scale is of axial distance from the argentea. (Modified from Land, 1965)

Menzel[224] opened a discussion in 1979 with the statement "A mollusc eye containing more than one photopigment has yet to be found." He then goes on to mention the meager amount of available data, the fact that virtually no intracellular recordings had been published, and the ERG data available tended to emphasize the dominant photopigment present. He then reviews the data, pointing out that no measurements in the ultraviolet were available and that two peaks were frequently measured at 475 nm and 540 nm, including those by Cronly-Dillon in 1966 [225]. Based on the model used here and the location of these two peaks, the data strongly suggests the presence of at least an M-channel and an S-channel chromophore in the mollusc eye. The peak at 540 nm. caused by the M-channel chromophore with a theoretical peak at 532 nm. The 475 nm. peak is due to the Bezold-Brucke Effect in the presence of both an S-channel chromophore with a peak at 437 nm. and the M-channel chromophore. The Bezold-Brucke Effect is normally reported at the psychophysical level. It is observable at the electro-physical level, especially when using a very high impedance (current) probe. A current probe introduced into the IPM is a low impedance device relative to its surroundings. As a result, it will sample and sum the currents from a group of nearby photoreceptors in an uncontrolled manner.

McReynolds & Gorman provide a comprehensive study of the signals emanating from the two retinas of *Pecten irradians*[226]. Lacking a credible model, they were unaware of how the eye actually operated. They suggest a 2-3 log unit difference in sensitivity between the two retinas while their imaging light was focused at the entrance aperture of only one of them. They presented considerable electrophysiological data but it is not at all clear which part of the various photoreceptor cells were probed. This leaves much of their data in conflict with other literature and the model presented here. The data in their papers are worth re-analyzing. However, the use of a high impedance probe must be accounted for and their imprecise specification of the probe location recognized.

1.7.2.3 *Chordata*

The chordate retina is the most widely studied. However, its geometric complexity soon leads to difficulties in interpretation and description. Because of this, most of the literature uses cartoons or statistics to describe the distribution of photoreceptors over the surface of the retina.

Figure 1.7.2-7 from Polyak shows the complex arrangement of the retinal elements at a large scale. It highlights the

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[224]Menzel, R. (1979) Spectral sensitivity and color vision in invertebrates. In Comparative Physiology and Evolution of vision in invertebrates. Autrum, A. ed. NY: Springer-Verlag pp. 537-540

[225]Cronly-Dillon, J. (1966) Spectral sensitivity of the scallop *Pecten maximus*. Science vol. 151, pg. 345

[226]McReynolds, J. & Gorman, A. (1970) Photoreceptor potentials of opposite polarity in the eye of scallop, Pecten irradians. J. Gen. Physiol. vol. 56, pp. 376-406 (Two papers)

presence of blood vessels on the surface of the reverse retina as well the paths of the optic nerve fibers on their way to the optic disk.

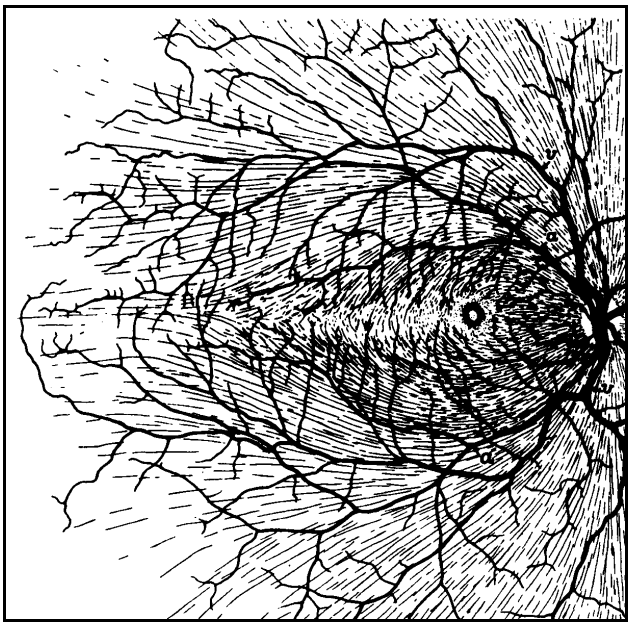

Figure 1.7.2-7 Drawing of the retina in rhesus macaque monkey. The thin lines show the pathways of the optic nerve fibers. The heavy lines are the blood vessels of the retina. The optic disk is at the far right; the fovea centralis appears as the encircled region to the left of the disk. (From Polyak, 1941)

Figure 1.7.2-8 from Pirenne[227] presents one of the best detailed photographs of the human retina available. It shows the relative size of the photoreceptors within the fovea, roughly the diameter of the circle, and outside the fovea. Unfortunately the section is taken through the IS. Fortunately, other less well oriented electron micrographs are available to determine the photoreceptor density in the OS. As a rule, the chordate eye is not sensitive to polarization of the incoming light. However, there may be exceptions. Waterman has described this polarization sensitivity[228].

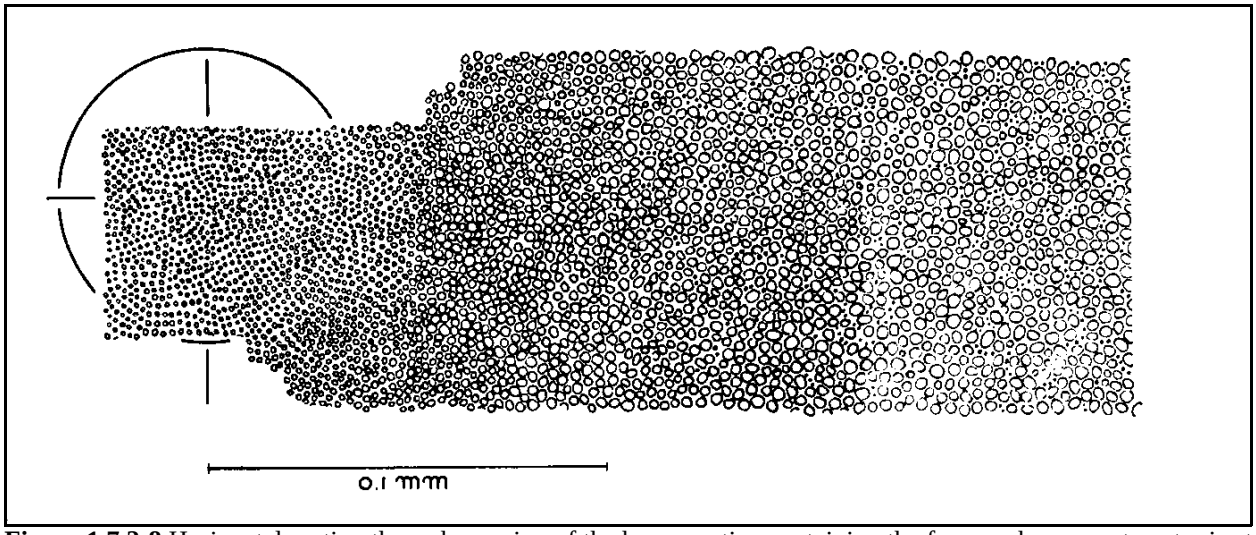

Figure 1.7.2-8 Horizontal section through a region of the human retina containing the fovea, whose exact center is at the intersection of the straight lines at left. The section is through the inner segments. (From Pirenne, 1948)

1.7.2.3.1 The multispectral chordate retina

The chordate retina consists of multiple arrays of photoreceptors with different spectral characteristics. In the general case, the total retina is tetrachromatic. This is true of all species of chordates. This fact is well documented among the fishes and aphakic humans. Although too narrow a position, Bennett & Cuthill said: "Humans are atypical vertebrates in being UV-blind[229]." They have provided a good (but demonstrably incomplete) discussion of the various species known to exhibit ultraviolet sensitivity. This sensitivity frequently rival or exceeds the sensitivity in other spectral bands. The ability to sense ultraviolet light is frequently curtailed by the attenuation of the ultraviolet radiation by the physical optics of the eye. This attenuation is proportional to the thickness of the element called the lens in chordates. Since this thickness is scaled with the size of the animal, the UV capability of larger chordates is usually restricted. Jacobs has documented the UV capability of one of the smaller mammals, specifically the gerbil[230].

Interestingly, Jacobs has recently presented a review of the color vision of primates which omitted any discussion of the UV sensitivity of the human retina[231]. This is diametrically opposed to the demonstrations of Tan and Stark (Stark himself being aphakic). See **Section 17.2** for their data.

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[227]Pirenne, M. (1948) Vision and the eye. London: Chapman & Hall pp. 28-29

[228]Waterman, T. (1975) Natural polarized light and e-vector discrimination by vertebrates. *In* Light as an ecological factor II. Evans, G. Bainbridge, R. & Rackham, O. *ed*. Oxford: Blackwell Scientific Publ. pp. 305-335

[229]Bennett, A. & Cuthill, I. (1994) Ultraviolet vision in birds: What is its function? *Vision Res*. vol. 34, no. 11, pp 1471-1478

[230]Jacobs. H. & Deegan, J. (1994) Sensitivity to ultraviolet light in the gerbil (*Meriones unguiculatus*): characteristics and mechanisms *Vis Res* vol 34(11), pp 1433-1441

[231]Jacobs, G. (1996) Primate photopigments and primate color vision. *Proc. Natl Acad. Sci. USA*. vol. 93, pp 577-581

The retinas of chordates all exhibit the same spectral sensitivity for each of their spectral channels. Baylor & Hodgkin provide excellent spectral data on the red-eared swamp turtle, *pseudemys scritpa elegans*[232]. The groups involving Neumeyer[233] and involving Douglas[234] have both provided data showing the tetrachromatic spectral responses of the fish. McFarland & Loew have recently provided data on marine fish[235]. These data all show the long wavelength spectrums peaking near 625 nm and Neumeyer specifically notes the incongruity of much of the literature claiming a spectral absorption peak near 565 nm (pg. 212). All four spectral peaks agree well with the peaks at 342, 437, 532, 625 nm predicted by this theory. Griswold & Stark have provided detailed spectral absorption characteristics for aphakic humans that also correlate with these peaks[236]. This capability will be discussed in detail in **Chapters 5** and **17** and is shown in the next figure. Neumeyer also explored the difference between the spectral performance measured by behavioral experiments and electrophysiological measurements. These differences are also explained by this theory.

Douglas, et. al. address the possibility that some fish may exhibit polarization sensitivity in their UV spectral channel.

1.7.2.3.2 The commonality of the spectra across Chordata

There is considerable confusion in the literature concerning the spectral and colorimetric performance of the visual systems found within *Chordata* (and recently extended into higher *Mollusca*). Contradictory views have been expounded upon with some vigor by accredited (but frequently uninitiated) members of the psychology and biology community as to the capability of chordate visual systems. The argument has two aspects, where man stands in the hierarchy with regard to perceiving color and where he stands in the hierarchy with regard to sensing spectral information. A careful review of the literature will demonstrate that the human system is actually tetrachromatic although its performance is limited largely to trichromacy by the absorption of the lens. This condition is shared by all large chordates. The fact that the retina is tetrachromatic is well documented by several investigators, one of whom is aphakic and exhibits excellent spectral sensitivity in the ultraviolet. More significantly, the data in **Figure 1.7.2-9** demonstrates the common spectral sensitivity of the visual systems (with the lens removed in the case of man) between adult humans and adult Zebrafish. The figure combines the data of Griswold & Stark with that of Saszik & Bilotta[237]. It should be noted that the sensitivity of ultraviolet wavelength spectral channel is higher than that of the short wavelength spectral channel in both species.

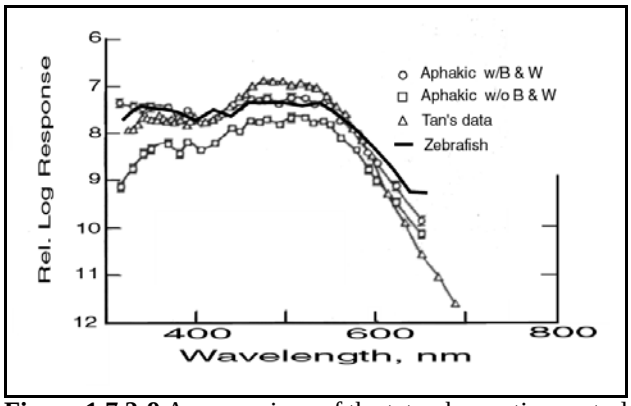

Figure 1.7.2-9 A comparison of the tetrachromatic spectral characteristics of humans and zebrafish. The heavy dark line is the mean of the spectrum of zebrafish presented by Saszik & Bilotta in 1999. Their range intervals are omitted for simplicity. The upper two lighter lines are the spectral capability of the adult human retina from two different investigators. The lower light curve is the result of using a different protocol in the data reduction process. (See **Chapters 5** & **17**).

The above data, the human data acquired psychophysically and the zebrafish data acquired by LERG located at the output of a bipolar cell in the luminance channel of the retina, unequivocally show the common spectral capability of these two diverse retinas. It is significant in the ultraviolet region.

The question of whether the different species use this information effectively to ascertain the color of an object will be addressed later in this work. However, a growing list of species, including many fishes, birds

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[232]Baylor, D. & Hodgkin, A. (1973) Detection and resolution of visual stimuli by turtle photoreceptors. *J. Physiol*. vol. 234, pp. 163-198, pg. 178

[233]Neumeyer, C. (1986) Wavelength discrimination in the goldfish. J. Comp. Physiol. vol. 158, pp. 203-213

[234]Douglas, R. Bowmaker, J. & Kunz, Y. (1987) Ultraviolet vision in fish. *In* Seeing contour and colour, Kulikowski, J. Dickinson, C. & Murray, I. *ed*. NY: Pergamon Press

[235]McFarland, W. & Loew, E. (1994) Ultraviolet visual pigments in marine fishes of the family, *Pomacentridae*. *Vision Res*. vol. 34, no. 11, pp 1393-1396

[236]Griswold, M. & Stark, W. (1992) Scotopic spectral sensitivity of phakic and aphakic observers extending into the near ultraviolet. *Vision Res*. vol. 32, no. 9, pp 1739-1743

[237]Saszik, S. & Bilotta, J. (1999) The effects of temperature on the dark-adapted spectral sensitivity function of the adult zebrafish. *Vision. Res*. vol. 39, pp 1051-1058

and mammals have been shown to respond to differences in the chromatic content of scenes presented to them. The conclusion appears inevitable that all chordates are multispectral in their sensing capability and once acquired, the data is used to perceive color.

A variety of investigators have asserted that humans are the only trichromatic mammals. However, their documentation frequently argues otherwise. Carroll et al. have recently provided partial data for the horse, *Equus caballlus*, that supports this position[238] based on their interpretation of Jacobs [239]. They assert the horse is dichromatic. However, Jacobs shows trichromatic sensing in figure 3.21 of his 1981 work[240]. Figure 1 of Carroll et al. shows clear signatures of the S–, M–, & L– spectral channels (note the distinct shoulder in the long wavelength region near 590 to 620 nm). They isolated the S–, and partially isolated the M– channel by differential adaptation using a broadband source and a long wavelength pass filter with a 50% point at 600 nm. However, they reported no effort to isolate the equivalent L– channel response by differential adaptation using a broadband source with a short wavelength pass filter with a 50% point in the region of 450 nm.

1.7.2.3.3 Polarization sensitivity of the normal retina

The first order retina of chordata is not sensitive to the polarization of the incident radiation because of the orientation of the chromophores associated with the individual photoreceptor cells. Most of the surface area of the chromophores of each disk is oriented such that the axes of the chromophore molecules are parallel to the long axis of the Outer Segment. These Outer Segments are in turn oriented toward the center of the pupil of the eye. As a result, the axes of most of the chromophore molecules are parallel to the Poynting vector of the incident light. This orientation offers no sensitivity to the polarization of the light.

Three second order conditions can provide some sensitivity to polarization. Experiments with polarized light have shown a slight degree of response to polarized light in the form of Haidinger's brushes. These are two faint perceived orthogonal brush strokes near the line of fixation. They are believed to be due to dichroic molecules associated with the macular pigment on the surface or in the bulk material of the INM. A similar phenomenon is known as Boehm's brushes. It is a transient phenomenon that can be optimally viewed when the e-vector of the incident polarized light is rotating at one rotation/second. It is probably due to intraocular scattering of the light. Waterman describes the effect as consisting of a cross with one arm dark and the other arm light relative to a neutral background when the source is a small spot of light. The third condition is found where the Outer Segments of the photoreceptors are not properly aligned toward the pupil of the eye.

Waterman has reported that some birds and many fishes exhibit a sensitivity to polarization in their peripheral retina[241]. Based on extensive behavioral experiments, it appears this capability is not an artifact but is used in routine life, probably for navigation. The detection of such radiation could be the result of the Outer Segments of the peripheral retina not pointing toward the pupil of the optical system. The Poynting vector of the incident light would not be parallel to the preferred absorption axis of the chromophores under this condition and a sensitivity to polarization could be expected. Such a distortion of the geometry of the retina has been documented as a pathological condition in humans (See **Section 3.2.2.1.1**).

Waterman states that no sign of polarization sensitivity could be found in the normal complement of retinal neurons when measured using normal S-plan measurement techniques. It is suggested here that such a signal might be found in the non amercine lateral neurons of the second horizontal matrix. However, the polarization signals probably do not represent a significant fraction of the total number of lateral cells in this matrix. Alternately, the signal processing required to generate a polarization sensitive signal of the bipolar type might be performed in the tectum. Waterman found polarization sensitive signals were quite common in the tectum. It is their origin that is still a mystery.

The sensitivity to polarization in the behavioral experiments was shown to be maximal along specific axes that were different for different neurons of the tectum. Frequently two sets of neurons were found exhibiting maximum sensitivity to orthogonal polarization axes. These axes were generally oriented parallel to the dorsal-ventral and the anterior-posterior axes. It was also shown that the sensitivity to polarization was minimal near the optical axis of the retina and increased with distance from the axis. Finally, he says that no signs of color specificity or adaptation

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[238]Carroll, J. Murphy, C. Neitz, M. Ver Hoever, J. & Neitz, J. (2001) Photopigment basis for dichromatic color vision in the horse *J Vision*, vol. 1, pp 80-87

[239]Jacobs, G. (1993) The distribution and nature of colour vision among the mammals *Biol Revs* vol 68, pp 413-471

[240]Jacobs, G. (1981) Comparative color vision. NY: Academic Press pg 4

[241]Waterman, T. (1975) Natural polarized light and *e*-vector discrimination by vertebrates. *In* Evans, G. Bainbridge, R. & Rackham, O. *ed.* Light as an Ecological Factor: II. Oxford: Blackwell Scientific Publications

phenomenon have been found associated with these polarization signals.

Waterman performed off-axis experiments that seemed to show the polarization sensitivity increased with distance from the focal point of the incident radiation regardless of the location of that point on the retina.

1.7.2.3.4 Polarization sensitivity of the *in-vitro* retina

When the outer segment of a chordate photoreceptor cell is exposed to transverse irradiation, it is highly polarization sensitive. This is due to the unidirectional orientation of virtually all of the chromophores on the surface of the disks. Loew has addressed this subject[242]. He shows that maximum sensitivity is achieved when the *e*-vector of the radiation is perpendicular to the long axis of the segment. He also notes the fact that the ultraviolet sensitivity of the Tokay Gecko was overlooked throughout his long association with Crescitelli in this area. He also notes the difficulty of defining rods and cones at the light microscope level so as to agree with their definition at the ultrastructure level.

1.7.2.3.5 Alternate fovea found among chordate retinas

Figure 1.7.2-10 shows the dual fovea capability found among a variety of predators, particularly predator birds[243].

Smith has reproduced a figure from Meyer showing a variety of fovea (historically described as pecten and more recently as areae centralis) among birds[244].

1.7.2.3.6 Unique retina reported in deep sea fishes

Several adaptations have occurred in fish eyes.

Fritsches et al. have reported on unique circulatory systems designed to maintain the eyes and associated musculature of cold-blooded fish near endothermic temperatures in order to maintain necessary performance levels[245].

A recent paper has provided interesting material on specialized retinas in many families of deep sea fish[246]. It suggests a special technique have evolved that crosses many family lines. The situation requires more study to come to firm conclusions concerning the operation of these eyes. The general finding is that the retinas of these fish contain multiple banks of outer segments going beyond the dual bank structure of *Pecten maximus* sited above. Banks of four through seven levels are reported. Locket has reported that the number of banks may change during the animals lifetime[247]. These species are normally moribund when brought to the surface. This fact suggests the need for very careful analysis to avoid incorrect interpretation of artifacts introduced due to the great change in pressure.

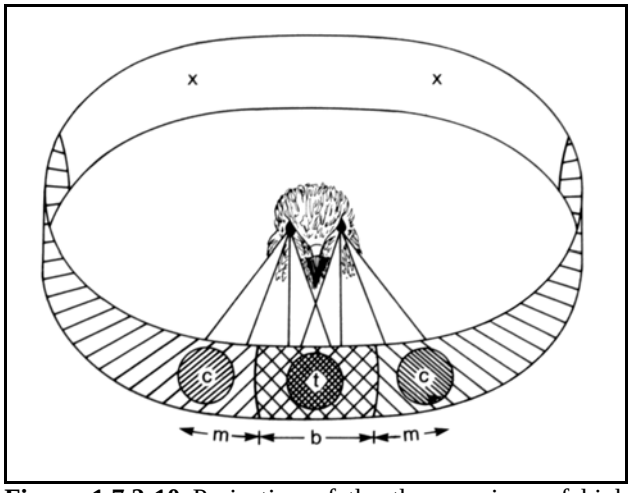

Figure 1.7.2-10 Projection of the three regions of high acuity in the visual field of a hawk. The central fovea of each eye project to monocular areas in object space. The temporal fovea project to an area within the binocular field. Stereo-optical vision can be expected within the region marked t. From Walls, 1967.

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[242]Loew, E. (1994) A third, ultraviolet-sensitive, visual pigment in the Tokay Gecko (Gekko gekko). *Vision Res*. vol. 34, no. 11, pp 1427-1431

[243]Walls, G. (1967) The Vertebrate Eye. NY: Hafner

[244]Smith, C. (2008) Biology of Sensory Systems, 2nd Ed. NY: Wiley-Blackwell pg 387

[245]Fritsches, K. Brill, R. & Warrant, E. (2005) Warm eyes provide superior vision in swordfishes *Cur Biol* vol 15, pp 55-58

[246]Frohlich, E. & Wagner, H-J. (1996) Rod outer segment renewal in the retinae of deep-sea fish. *Vision Res*. vol. 36, no. 19, pp 3183-3194

[247]Locket, N. (1980) Variation of the architecture with size in the multiple-bank retina of a dee-sea teleost, *Chauliodus sloani*. Proc. Roy. Soc. London, B. Vol 208, pp 223-242

Frohlich & Wagner noted the thinness of the typical retina in deep-sea fish. However, their figure 1(a) shows outer segments scattered over a depth of 250 microns, far beyond the depth of field of the optical system, and highly disordered. It appears this view may be a cross section of the retina at a shear angle. The major elements appear in cross section as ellipsoids instead of the normal rectangles. The images do not suggest the presence of multiple banks of outer segments or of the neural connections required to support them. The text of their figure 1(b) suggests the rods are longer than in 1(a) and arranged in two banks. However, the figure appears to show the inner and outer segments of a conventional retina not unlike that of Boycott and Dowling and shown in **Figure 3.2.1-1**. The ends of all of the outer segments (at the inner segment interfaces), in 1(b), appear to be in a plane with a tolerance of less than 10 microns relative to the Petzval surface of the lens. This tolerance would be compatible with the depth of focus of the optics of deep-sea fish. No such single focal plane appears possible in figure 1(a).

1.7.2.4 Categorization of retinal systems

The discussion in **Section 1.7.1.5.5** can also be used to create a consistent set of names for the retinal components of the eye of the three phyla of interest here.

Chordata	*Arthropoda*	*Mollusca*	Comment
Retina	Retina	Retina	In all compound and complex eyes
	Retinula		In simple eyes, corresponds to one rhabdom
	Rhabdom	Rhabdom	A group of related photoreceptor cells
Photoreceptor cell	rhabdomin	rhabdomin	A photoreceptor cell (less the Outer Segment)
Outer segment	rhabdomere	rhabdomere	The segment containing the chromophore
Inner segment	part of rhabdomin	part of rhabdomin	Contains Golgi apparatus, etc.
Soma	part of rhabdomin	part of rhabdomin	Contains the nucleus, and other machinery of the cell
Tapetum	basal pigment	Argentea	A residual light absorber or reflector

1.7.3 Generic oculomotor systems

As indicated earlier, *Arthropoda* and *Mollusca* both use an eye that is fundamentally body mounted. There are no muscles to provide a motor function in these eyes, excepting possibly *Cephalopoda.* Convergence may have produced some motor capability in this species. This motor capability is limited to vibrating the eye relative to a hinge point formed by the crossover in the neural bundle, See **Section 1.2.1.4**.

The motor capability of the chordate eye is extensive and sophisticated but not well studied because of the instrumental complexity involved. Most of the available data is from Man or from rhesus monkeys, with some data available from cats. Schiller[248] has provided a review and some very good data that can be interpreted more precisely using the model presented here. He probed a group of neurons in the abducens nucleus of monkeys and correlated this data with ocular motion using electro-oculo-graphic techniques, EOG. These techniques do not normally record the tremor phenomena. It does not appear that Schiller recorded the actual drive signals from the final neurons controlling the oculomotor muscles nor did he offer any model of the Precision Optical System of which the abducens nucleus is a part. Schiller does develop the fact that there may be as many as four different systems controlling eye movement. **Section 7.3** of this work will show that the oculomotor system consists of two functionally separate parts, the neural sensing and command instruction part and the neural command implementation and muscular response part. Each of these major parts may involve distinct sub systems depending on species requirements.

1.7.3.1 Motor system of Man

The critical importance of the motor system to the performance of the human visual system has not been fully appreciated. Although it has been well established since at least 1940 that motion of the scene as a function of the line of sight is critically important to vision, the motor system has been studied only superficially. The problem of quantifying the performance of this system was due primarily to the limited capability of the available instrumentation. However, with time it became ever more obvious that these motor mechanisms were critically

[248]Schiller, P. (1970) The discharge characterisitics of single units in the oculomotore and abducens nuclei of the unanesthetized monkey. *Exp. Brain Res*. vol. 10, pp 347-362

important. Alpern wrote in 1962[249]: "Measurements of these effects began around the turn of the century but considerable doubt as to the facts persisted until relatively recently and it is only with the last few years that the full importance of the process is beginning to become clear. . . . It will suffice to point out that the constant involuntary movements of the eyes under steady fixation are prerequisites for normal vision. Thus, in a very real and important way, vision is dependent upon and requires movement." Similar words have appeared subsequently but without a comprehensive presentation on how and why these movements of the motor system are critical.

Section 7.3 of this work provides the first comprehensive discussion of the mechanisms and performance of the motor system in man and its impact on his vision. The system involves a dual capability high performance closed-loop servo-system of the sampled-data type. The system is critically dependent on the portion of the midbrain previously described as the auxiliary optical system. This complex of neural centers is redefined here as the Precision Optical System (POS). The designation recognizes its importance in vision.

The overall servo system necessarily operates in the sampled-data mode because of the conversion of the analog signals from the retina into pulses encoded in time before their transmission over the optic nerve to the midbrain.

The eyes of man are essentially spherical gel filled solids for purposes of displacement and rotation. They rotate about a point nearly identical with the optical center of the eye. Each eye is supported by three pairs of muscles as shown in **Section 2.4.** Although the muscles are not orthogonal in their mechanical configuration, nearly orthogonal motion is achieved in azimuth and elevation through the use of the third set of muscles. This set provides an incremental correction based on motor signals calculated in the midbrain. This independence of azimuth and elevation motion provides repeatability in pointing, despite the previous fixation angles according to Listing's Law. The motor calculations in the midbrain, associated with stereo-vision perception, also assure proper parallax compensation. The overall muscle system does contribute to rotation of the eye around the line of fixation. Rotation is essentially zero along the azimuth plane and the elevation plane. For details, see data from Helmholtz in Southall[250] or a more detailed reprint by the JOSA[251].

The dynamics, as opposed to the kinematics discussed above, of the motor mechanisms of vision have not been widely discussed elsewhere. Comprehensive discussions of the mechanisms supporting the dynamics of the motor system are very difficult to find.

The dual capability of the oculomotor portion of the overall system is clearly exhibited in the dual character of the muscle tissue controlling the rotation of the eyes. These muscles are controlled by two distinct servo systems, the outer wide angle, but coarse system and the inner small-angle high-performance system. The inner system operates with a bandwidth of above 120 Hertz while the inner system typically operates below 30 Hertz.

The wide angle but coarse capability of the outer servo loop of the oculomotor system is highly integrated with the overall motor system. This allows anticipation of the motions of the head and body while pointing the eyes relative to the head. It is used primarily to insure that the individual is fully aware of and able to evaluate his surroundings. Much of this function is achieved without the participation of the cortex because of the excessive time delays involved in transmitting signal to the cortex for processing. The evaluation is performed by the POS.

The POS is also critical to the human when extracting precise information from the imagery presented to the foveola by the outer servo-loop. **It is this precision capability that allows humans to interpret fine detail and to read.** The capability of the human to read and the performance of the overall visual system will be presented in detail in **PART D** and **PART E**.

The requirement for motion between the image and the line of fixation of the eyes is a clear indication that the human eyes are not pixel-based framing cameras as so often described in elementary vision literature. The human eyes are based on an underlying change detection technology. It is this underlying change detection technology that achieves the super-resolution measured for the eyes compared with what would be achievable with a pixel-based system.

Comprehensive discussions of the *results* of measurements on the motor mechanisms are available. The dynamics can be segregated into at least four categories, with slight differences in the parameters between azimuth and elevation. These categories and their operation in Man are;

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[249]Alpern, M. (1962) in Davson, H. *ed*. The Eye, Vol. 3. NY: Academic Press pg 72-76

[250]Southall, J. (1961) Introduction to Physiological Optics. Reprint of 1937 edition. NY: Dover Publications pp. 164-179

[251]http://poseidon.sunyopt.edu/BackusLab/Helmholtz/ (A JOSA reprint of Southall's 1924 translation of Helmholtz's original 1910 treatise.

Name	Control	Purpose	Range	Velocity
Large saccades	largely voluntary	tracking	many deg	400-700 deg/sec.
Small saccades	involuntary	tracking field analysis	5.6 arc sec	10 deg/sec.
Slow drifts	involuntary	open loop drift of muscle system	5 arc min	1 arc min/sec
Tremor	involuntary	search field imaging	20 arc sec	50-90 Hertz

The large saccades are obviously used to redirect the line of fixation within the large angular range available in the human eye. Several studies have shown the small saccades are used to scan the fixated image, much like a vector scan. If the visual system is not concentrating on a fixated image, an open loop drift of the line of fixation occurs. This drift is corrected periodically by a movement similar to a small saccade. Finally, the Tremor is a continuous oscillatory motion except during intervals occupied by the large and small saccades. It is not needed during the large saccades as the brain disconnects the visual memory from the signals generated by the eye during such motion. More work is needed to learn whether the Tremor exists simultaneously with the small saccades.

It is the author's experience that tunnel vision resulting from fatigue is caused by the failure of the eye muscles to maintain the amplitude of the tremor. The diameter of the tunnel is approximately the same as the diameter of the fovea.

1.7.3.2 Motor system of other chordates

The organization of the muscles associated with the eye is generally the same in other chordates as in Man. As indicated briefly earlier, many vertebrates seem to control tremor, either voluntarily or subconsciously during their normal activities. It appears they can decrease the amplitude of the tremor to control the signal processing load on the brain (and to a lesser extent the retina). As the tremor amplitude is reduced, the sensitivity of the peripheral retina to fixed images is decreased without significantly reducing the sensitivity to motion in the periphery. If the animal has a fovea, the sensitivity of this region to nonmoving imagery is not reduced until the tremor amplitude is reduced to less than the size of an individual photoreceptor. The perceptual result is similar to a scene with the information in the center highlighted by a spotlight. If the animal does not have a fovea, the sensitivity to nonmoving imagery is reduced compared with moving imagery everywhere in the field of view as the tremor amplitude is reduced.

1.7.3.3 Motor system of non-chordates

The basic eye of *Mollusca* is body mounted and no muscles are associated with the rotation of the line of sight of the eye. However, *Cephalopoda* appears to have moved, or be moving, toward a limited degree of eye motion. Although the resulting motion is not rotary as in *Chordata*, it does provide limited motion about a pivot point external to the eye. The resulting slight angular motion of the line of sight appears adequate to allow the perception of stationary imagery within its normal field of view. Such perception would only be realized if the eye muscles provided a tremor as in Chordata. No data could be found concerning the structural dynamics of the cephalopod eye.

1.8 Generic visual subsystem based on neural topology

The neural system of the three phyla vary considerably based on their ecological nitch and subsequent development of what can be described as the central nervous system, CNS, or brain. The development of the brain progresses from *Insecta*, through *Mollusca* to *Chordata*, with some interesting near overlaps in capability near the margins of each Phylum.

The following material on the neuron is applicable across the phyla. The topological material on the neural system will focus on *Chordata* as including the broadest capabilities, and of greatest research interest.

1.8.1 Generic neuron; the mechanisms and operation of

The neuroscience community has not been able to describe the fundamental mechanism underlying the operation of individual neurons, Nodes of Ranvier and synapses during the last 100 years. This is amazing in the light of progress made in other fields. The problem can be traced to the adamant position taken by the majority of the community that the neural signaling system is chemically based. The problem has been sustained by the failure of the community to embrace modern semiconductor physics as it applies to the liquid crystalline structure of most biological tissue. This work will show that the neural signaling system can be described in great detail on the assumption that it is electrolytically (rather than chemically) based. The analysis leads to the description of the active electrolytic semiconductor (transistor) device known as the ACTIVA. It also shows that each synapse, each Node of Ranvier and the active mechanism within the soma of each neuron contains an ACTIVA.

Because of the radical paradigm shift proposed by this work concerning the neuron, selected material will be presented here to assure the reader of the viability of the proposal. References are provided to other sections where the subjects are developed in detail.

1.8.1.1 Overview of a neuron

The fundamental architecture of the neurological system of all animals is very simple. It consists of a large array of afferent signal paths converging on the cognitive elements of the central nervous system and a similar set of efferent signal paths connecting to the muscles of the animal. Each of these signal paths consists of a series of short conducting elements separated by active amplifying devices. The system is entirely electrolytic. The system is supported by a variety of morphological structures to support the growth and metabolism of the system. An argument has been ongoing for years over the role of chemistry versus electronics in the signaling function within the neurological system. This controversy has been fueled by two factors. One has been the limited spatial resolution of the techniques available to the morphologist. The second has been the broader background of most biologists in chemistry. However, when these barriers are surmounted, the fundamental nature of the neurological system is easily determined.

Each of the conducting elements is a conduit consisting of a biological membrane enclosing an electrolyte and surrounded by a second electrolytic medium. The surrounding medium may be an additional compartment within the same cell that is also surrounded by a membrane or it may be an extracellular medium. These electrolytes are generally known as neuroplasms. There are three primary subcategories, the axoplasm, the dendroplasm and the podaplasm. The last name is new to the literature. It is related to the fact that the active devices of the neural system are three terminal devices. Differentiating the neuroplasms associated with the input terminals of these devices by distinctive names is desirable. As will be seen below, the dendroplasm is associated with the non-inverting input terminal of the active device and the podaplasm is associated with the inverting input terminal.

For the last fifty years, the active device within the neurological system has assumed to be a two terminal device, the external membrane surrounding the axoplasm of a cell. As science has progressed, it has become clear that the membrane of the axoplasm is a very simple structure that does not exhibit activity (excitability in the literature) capable of signal amplification. Signal amplification in the electronic sense is key to the operation of a signaling system. This work will show that signal amplification is achieved in the neural system by a form of "transistor action" similar to that widely used by man-made devices. The discovery of "transistor action" occurred at almost the same time that Huxley, Hodgkin and Katz were defining the axolemma as the excitable element in the neuron. However, it was not explored successfully by the biological community although organic chemists have been seeking to identify it in electrolytic chemical systems for a long time.

1.8.1.1.1 Top level representation of the stage 2 signal processing neuron

Figure 1.8.1-1 provides an initial expansion of the stage 2 neuron in the block diagram of **Section 1.5.1.2.2**. It is a *preview* of the signaling portion of the neuron based on "The Electrolytic Theory of the Neuron;" the fundamental new theory of neural operation replacing the previous chemical theory of the neuron. After exploring the relevant physics of The Electrolytic Theory of the Neuron, the details of the neuron will be explored in detail in **Chapter 10**. In this figure, a variety of elements need to be introduced before the functional organization of the retina can be introduced in **Section 1.7.5**.

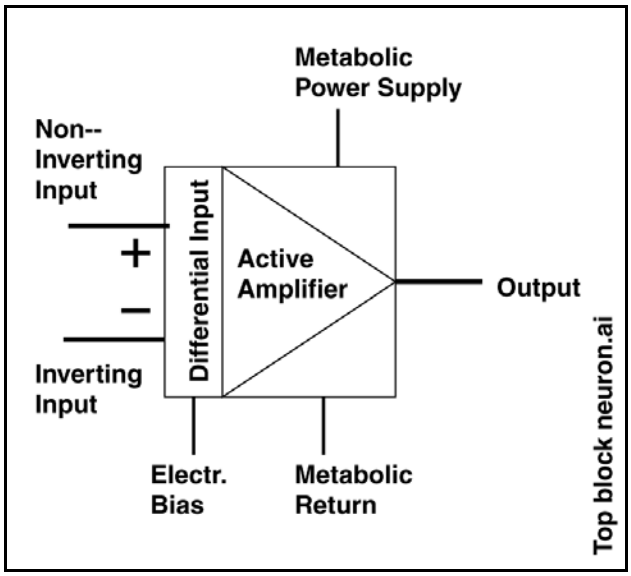

Figure 1.8.1-1 Top level representation of the signal processing neurons used throughout the neural system, based on "The Electrolytic Theory of the Neuron." See text.

The fundamental feature of the elements within the rectangular box is that they are all electrolytic in character. No chemical processes are involved in signaling, although certain chemical equations may be re-balanced due to a change in the electrolytic potentials arising in signaling.

The triangle within the box uses standard nomenclature for a differential amplifier of electronics. It includes an active electrolytic device, an *Activa*, which is a true biological analog of the man-made transistor.

The rectangle to the right of the triangle is superfluous, but included here for clarity. It stresses the fact that a neuron includes a three terminal signaling device plus auxiliary terminals. The three fundamental terminals are,

1. An output terminal, the pedicle of the axon.
2. A non-inverting input terminal, where the output terminal reproduces the input waveform ***without*** *a change in polarity*.
3. An inverting input terminal, where the output terminal reproduces the input waveform ***with*** *a change in polarity*.

There are three additional terminals,

4. An electrical bias terminal, frequently found but not required, to adjust the quiescent direct current potential at the output terminal in the absence of a "signal" at both inputs. Since the neuron is basically an analog, direct-coupled signaling device, the signals at the input terminals may consist of a direct current potential and a alternating current potential representing the signal information.

The final two terminals form the interface of the electrolytic neuron and the external, chemical, environment. Not shown in detail, but developed in detail in **Section 8.6.2**, is the electrostenolytic power conversion process at the external surface, lemma, of the neuron. This process converts a chemical , glutamic acid (glutamate) into a chemical known as gamma-amino butyric acid, GABA, with the release of two constituents; a carbon dioxide molecule into the external environment and a free electron into the interior of the neuron (**Section 8.6.2.3.3)**. The accumulation of such electrons inside of the neuron are the source of the negative potential found in all neurons (**Section 8.6**). In fact, this process is the source of the negative potential within all cells of biological tissue.

5. An acceptance terminal for glutamic acid on the external membrane, lemma, of the cell.

6. A release terminal for GABA and carbon dioxide on the external membrane, lemma, of the cell.

In total, ***the nominal signaling function of the neuron involves six terminals***. The last two are functionally combined at one electrostenolytic receptor site on the cell lemma.

The active electrolytic device found in the neurological system involves the convergence of at least two electrolytic conductors in a unique physical relationship that fosters "transistor action." The result is a three terminal active electrolytic semiconductor device found throughout the neural system and known as the Activa®. Activas occur at every junction between two or more electrolytic conduits within the neural system that meet a specific set of spatial requirements. Morphologically, these junctions are found within the Soma of a cell, between segments of the axon of a cell and between cells. However, they are not subsidiary elements of a cell. They, along with the conduits, are the primary signaling elements of a neurological cell (the neuron). All of the other functional elements of the neuron are there to *support* the signaling function provided by the conduits and Activas. These active devices are found at three morphologically identifiable sites in the system. They are the synapses between cells, the Nodes of Ranvier between segments of the axons of an individual cell and the previously unnamed, but electrically identified Activa within the cells. This Activa is generally associated morphologically with the hillock of a neuron. Functionally, it is the junction between the axoplasm , the dendroplasm , and the podaplasm of the cell.

1.8.1.2 Schematic of a bipolar cell, a neuron

Ignoring the metabolic and other housekeeping functions of a sensory neuron, its purpose is to receive one or more stimuli, process the information associated with those stimuli and deliver an output signal representative of the result. This signal can then be used as the stimulus to an orthodromic neuron. The processing is accomplished by an active device that can be described as a biological electrolytic semiconductor device[252] and is named an **Activa™**. In its basic form, the device exhibits three electrical terminals. The poda (or common) terminal joins the well recognized dendritic and axonal terminals. The poda corresponds to the base in solid state semiconductors. The dendritic terminal corresponds to the emitter and the axon corresponds to the collector terminal. **Figure 1.8.1-2** shows how the bipolar cell consists of an outer cell membrane and additional interior membranes. Each membrane contains a number of specialized regions. These will de discussed in detail in **Chapter 8**. In the very narrow region of the Activa, a unique condition exists that results in "transistor action." If the appropriate voltages are applied to the various electrolytes associated with the Activa, a current injected into the emitter of the Activa from the dendritic terminal will appear at the axonal terminal under significantly different impedance conditions. This constitutes electrical signal amplification although the output voltage at the axon may not be much higher than at the dendritic terminal.

[252]U. S. Patent #5,946,185

The appropriate voltages obtained from the literature suggest that all of the biological electrolytic semiconductor devices used in vison are of the “pnp” type. It can be assumed that all of the Activas of the neural system are of this type.

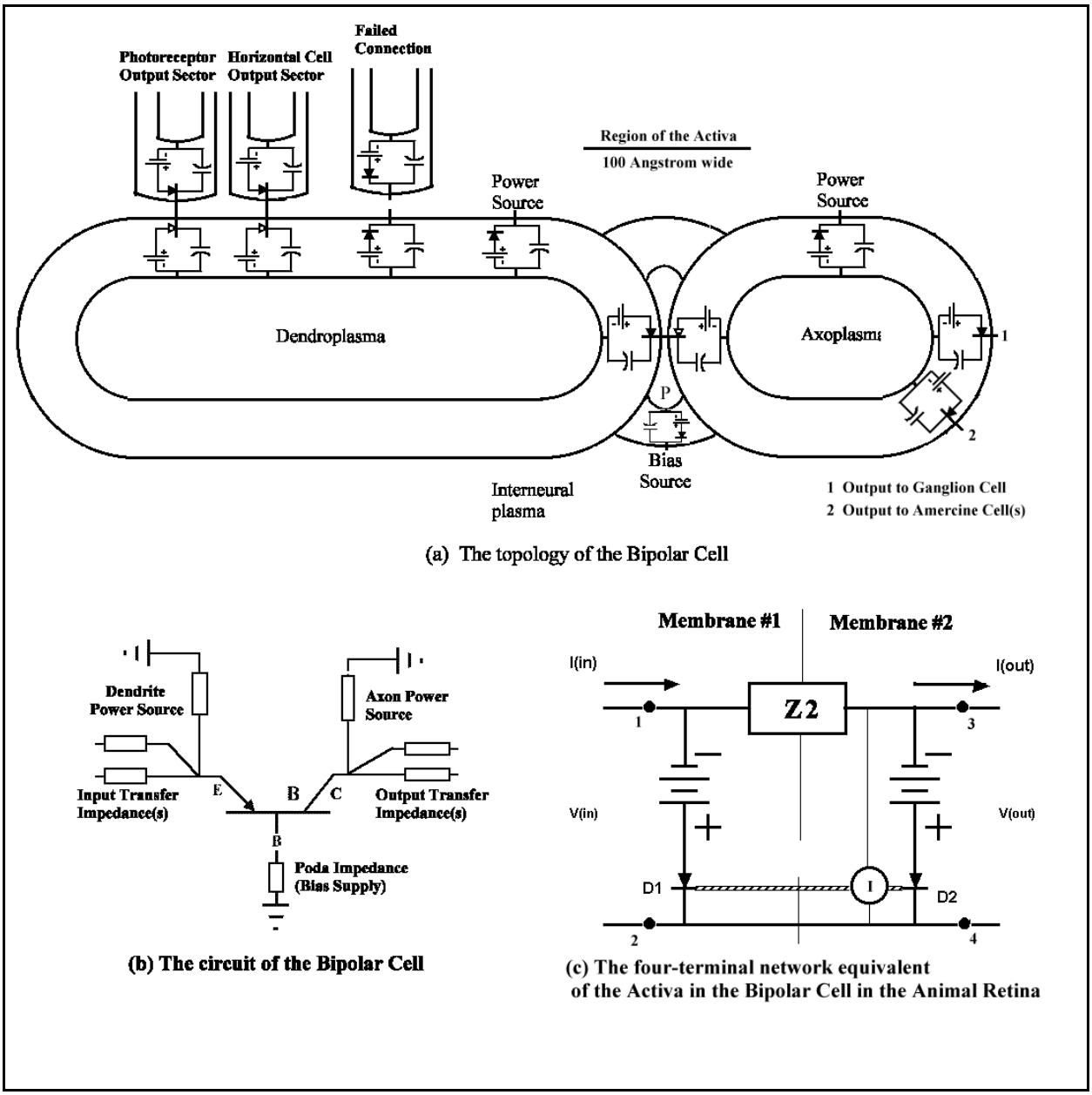

Figure 1.8.1-2 The combined topology and cytology of a bipolar cell and the resulting electrical circuit.

The details of the different Activa types and their typical quiescent characteristics will be found in **Chapter 10.** Their operating characteristics and applications will be discussed in Chapter 12 through 15.

Looking more closely at the neurological features of the visual system, several important facts are seen, and will be reported in detail in later chapters. The fundamental fact is that the neurological system related to vision is an electronic system. Following the pedicles of the photoreceptor cells, the fundamental signal is an electrical voltage modulated in a variety of ways. The signals are not directly related to chemical processes either within the cells or at the junctions between cells. The key to the operation of the neurological system is the biological transistor or

Activa. Each neuron contains one or more Activas. The signal carrying junction between two neurons is also a biological transistor, or Activa. Without the discovery of the semiconducting properties of the Activa, it was impossible to understand the operation of the neural system in detail.

In the body of this work, symbols drawn from the electronics field will be used to describe the actual circuit functions within the visual system. These symbols are meant to be *graphic representations of the actual bioelectronic circuits*. Many investigators will find it difficult to accept this representation and will prefer to think of the symbols as representing an electronic analog of the actual visual process. That is their choice. However, the following diagrams do not describe simulations or emulations of the neural system. They describe the neural system itself.

1.8.1.3 The synapse

As outlined above, the synapse is only one of a group of neural structures containing an active electrolytic semiconductor device known as an ACTIVA. These devices are also found in the soma and at Nodes of Ranvier. The active portion of the synapse is formed by a combination of physical, chemical and electrical conditions. The physical conditions involve the positioning of the membranes of two electrical conduits in extremely close proximity (less than 10 nanometers) to each other. In the case of the synapse, the conduits are known as the axon, and either a dendrite or a podite. The small spacing squeezes virtually all other chemicals out of this gap except for water. The water molecules form a liquid crystalline structure called hydronium in this space. If the two membranes are made of two symmetrical bilayers, as in most plasmalemma, no electrical action is possible, the materials act as insulators. In this case, the physical structure is known as an adherent junction. If however, the two membranes contain bilayers that are asymmetrical at the molecular level, they each represent an electrical diode. The application of appropriate electrical biases between the plasmas within the conduits and the hydronium crystal within the synapse will create an ACTIVA. Under these conditions, the ACTIVA acts as a perfect electrical diode between the presynaptic and post synaptic membranes (terminals). The result is a very low impedance electrical pathway between the plasma of the two conduits, a synapse. This pathway is unidirectional under homoeostatic conditions. However, the direction can be reversed under pathological conditions introduced by laboratory experiments. The complex nature of the synapse is discussed from a morphological perspective (**Section 4.3.6**), a chemical perspective (**Section 7.7.2**) and a functional perspective (**Chapters 8** & **9**, and specifically **Section 9.4**) in this work. Additional information is provided using the Node of Ranvier as a template in **Section 10.8**. The role of the Activa within the soma is addressed in **Section 10.6**.

1.8.1.4 A framework for discussing neurotransmitters and neuroactive substances

Over the years, the pharmacology community has developed a long list of materials that affect the operation of neurons. Lacking an appropriate framework, and relying upon the archaic neuron doctrine, they have attempted to describe all of these materials as neurotransmitters. They have also attempted to assign them all roles within the neural junction called a synapse. This has led to a chaotic situation with dozens of materials putatively being secreted by presynaptic terminals and causing actions at the nearby post synaptic terminal. Most of these materials are not neurotransmitters but either neuro-facilitators or neuro-inhibitors. This subject is discussed in detail in **Section 7.7**.

1.8.1.4.1 The electron and “hole” as true neurotransmitters

The only true neurotransmitter (the signal carrying medium passing between the conduits labeled variously as axons, interaxons and neurites--both dendrites and podites) is the electron. The electron actually moves through what is widely observed as “hole” conduction. It moves from ion-to-ion within a liquid crystalline lattice under the influence of an electrical potential bias. The net effect is that of a positive charge, a “hole” moving in the opposite direction.

Hole conduction is used in the electrolytic transmission of signals in the nervous system because liquid crystalline neural membranes are impervious to large ions, such as sodium, potassium and large molecules, such as glutamate and GABA. These materials only pass through specialized portions of neural membranes at very low rates.

1.8.1.4.2 Primary neuro-facilitators and neuron-inhibitors

The neurons are powered through a special electrochemical process occurring on specialized areas of the plasma membranes of neurons. The process is known as electrostenolytics. It involves a chemical reaction that produces a free electron and releases CO_2. The process is stereo-specific and only accepts two amino acids as a reactant. The primary reactant is glutamic acid (α-amino glutaric acid). The reaction product is commonly referred to as γ-amino butyric acid (GABA). The terms α and γ are essentially interchangeable in these materials. Historically, they were selected using different naming conventions.

As in most critical biological chemical reactions, there is a backup reaction. This reaction accepts aspartic acid in place of glutamic acid. Glutamic acid and aspartic acid are commonly called glutamate and aspartate within the pharmacology community. The words are easier to say. However, these materials are not salts in the chemical sense.

1.8.1.4.3 Other neuro-facilitators and neuron-inhibitors

Most of the materials previously labeled neurotransmitters are used differently than reported in the literature. Their action is to interfere with or enhance the above electrostenolytic process. If they are stereo-chemically appropriate they can interfere directly with the glutamate-GABA reaction. If not, they can interfere indirectly by affecting the diffusion of the principal reactants or other relevant parameters.

1.8.2 Generic Neuron Signaling System

This section will make a distinction between the neuro-motor system and the neuro-sensor system of an animal. The signaling system within the neuro-motor system commonly employs pulse transmission, i. e., action potentials. This is frequently not the case in the neuro-sensory system, particularly of the lower animals. These frequently employ only analog signals. The distinction blurs in some primitive animals, such as Limulus, where a neuron very close to the photoreceptor cells act as the transition point between the sensory and motor systems and generates an action potential. This is a unique situation that will be developed in detail in an appendix.

In the chordates, the neuro-sensory system is so physically extended that a signal projection capability is incorporated into the neuro-sensory system. This projection system employs the same signaling techniques as the projection system found commonly in the neuro-motor system. However, all signal processing is still accomplished in the analog domain.

The remainder of this Section will be restricted to the neuro-sensory system of animals.

1.8.2.1 The physical architecture of the neural system

The complexity of the neuron signaling system begins very simply and elaborates significantly with position in the phylogenic tree. There are very simple animals where the photoreceptor cell of a photospot connects directly to a muscle cell. Slightly higher up the tree intermediate cells are introduced.

Figure 1.8.2-1 shows that all bilateral animals, beginning with planaria, share a common top level morphological architecture for their neural systems. The central nerve cord is in itself bilateral as shown. The primary differences are two. A feature primarily of morphological interest is the degree of calcification of the capsule surrounding the nerve cord. Unfortunately, this criteria does not lead to a clear differentiation between phyla. The second criteria is based on the relative abundance of neurons in ganglia spread out along the nerve cord, rather than being grouped in a centralized brain. The extreme simplicity of the most primitive bilateral, *Planaria*, is illustrated. Members of *Arthropoda* and *Mollusca* have highly knots of neurons, ganglia, distributed along their nerve cord. In the case of *Mollusca*, only three are normally found. In *Arthropoda* and *Annelida*, the number of ganglia are usually coordinated with the number of body segments. Members of *Chordata* have the vast majority of their central signal processing (Stage 4) and signal distribution (Stage 3) neurons centralized within their cranium.

Note the frequent crossovers between the nerve cord of Planaria. This ladder-like arrangement becomes less important with progression up the phylogenic tree. In the more complex non-chordates, neurons are grouped in ganglia located periodically along the nerve cords. It is likely that both stage 3 signal relay and stage 4 signal processing occurs within these ganglia.

While all bilateral animals show left-right bilateral symmetry, some members of *Annelida* also exhibit top to bottom symmetry as well. The leech, *Hirudo, medicinalis* is noteworthy for having two brains, one located at each end of its nerve cords[253].

The morphology of the neural system is frequently obscured when speaking of Chordata because of the tendency to show a single spinal cord encased in a single column of vertebrate. This is misleading, the nerve cord of humans and other members of Chordata consist of a symmetrical pair of cords within the vertebra of the spinal column.

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[253]Kristan, W. et. al. (1974) Neuronal control of swimming in the medicinal leech (three papers) *J Comp Physiol* vol 94, pp 97-119, 121-154, 155-176

Oyster (referencing Martin, 1996) illustrates this fact and adds more detail[254]. Afifi and Bergman provide detailed caricatures[255]. The gross morphology is the same as in the lower animals. The transverse neural paths appear to be much less important in Chordata since the organism relies more heavily on the central nervous system to define more complex, and frequently non-repetitive, responses to specific threats.

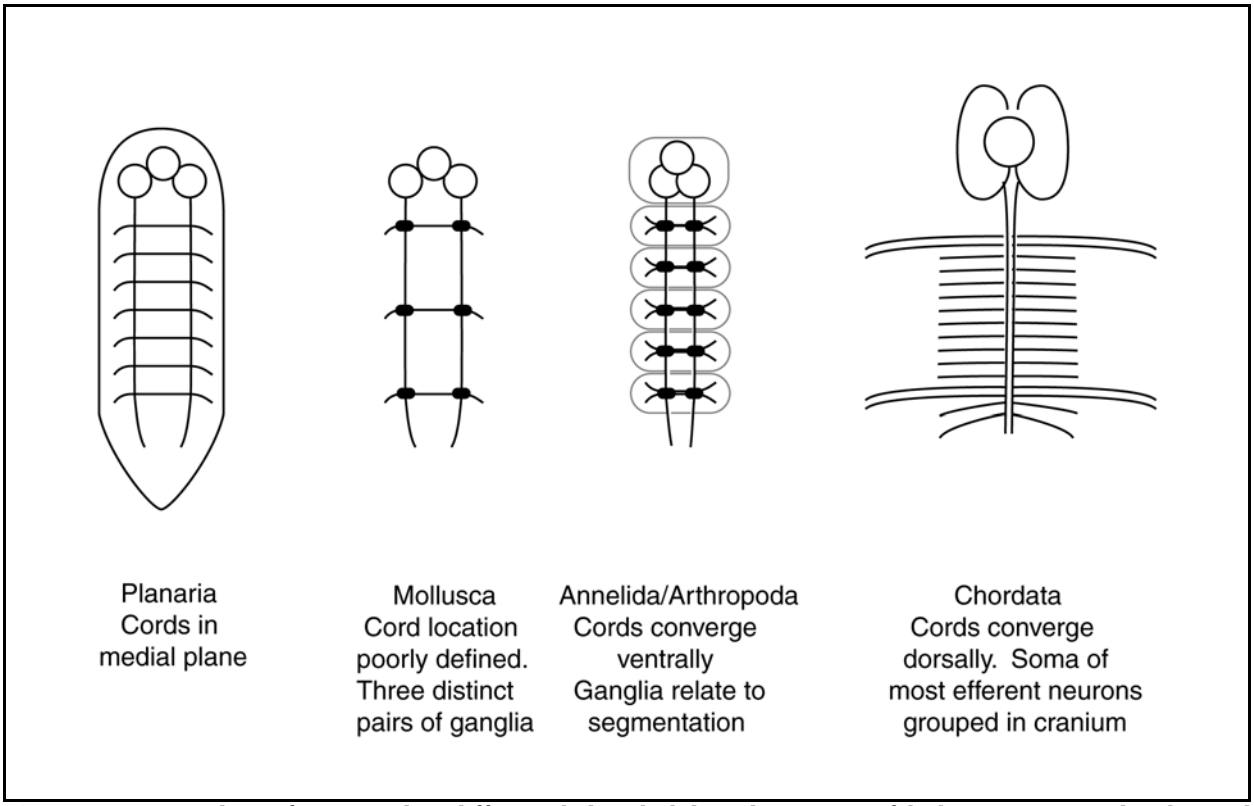

Figure 1.8.2-1 Topology of nerve cords in different phyla. The bilateral symmetry of the human nerve cord is obscured by its enclosure with the spinal column.

The visual portion of the neural projection system of an animal can be viewed from two perspectives. These are the physical architecture of the system used to achieve structural independence of the eye from the body (or head) and the signaling techniques used to extend the distance between the eye and the brain. The physical architecture of each phylum is different. In *Arthropoda*, the eye is usually firmly mounted to a specific body segment (not necessarily the head as we know it). In *Mollusca*, some small degree of structural agility is frequently found between the eye and the associated body part. However, it is only in rare cases, the heteropod *Pterotrachea coronata* as an example, that significant agility has evolved. In *Chordata*, a great degree of agility between the eye and the major body part has been achieved. However, this has required special neural projection architecture not broadly shared with the other phyla.

The physical architecture of the higher chordates is tailored to achieve rotational freedom of the eyes relative to the head. This is achieved by performing a large amount of signal processing within the retina and adopting a complex spatial and temporal signal encoding plan. This allows the optic nerve to be thinner compared with its length and therefore more flexible.

Signal manipulation within the neural system is carried out entirely in the analog domain[256]. However, as the size of the animal increases and/or the performance demands increase, the transmission of analog signals in the electrolytic

[254]Oyster, C. (1999) The Human Eye. Sunderland, MA: Sinauer Associates, Inc. pg 229
[255]Afifi, A. & Bergman, R. (1998) Functional Neuroanatomy. NY: McGraw-Hill pg 65
[256]There have been reports of digital mode signal processing in the peripheral nervous system but these were not supported by a model.

environment becomes time consuming. To overcome this problem, a separate and distinct mode of signal projection over long distances (greater than a tenth of a millimeter) at much higher speed is introduced. This signal projection mode employs pulse transmission over an electrolytic cable (typically the extended part of an axon). This pulse transmission mode is the source of the action potential of electrophysiology. Pulse transmission over an electronically simple electrolytic cable with the dimensions of an axon introduces a problem. Time dispersal in the projected waveform leads to a loss in signal amplitude with distance. To overcome this problem, the signal must be regenerated at regular intervals (of about a millimeter). This is accomplished by providing an Activa at intervals of between one and two millimeters over the entire length of the signal path. Such a path may extend for several meters. These regenerative repeaters are known morphologically as Nodes of Ranvier.

As the complexity of the animal increases, it becomes necessary to perform signal processing at various stages in the signaling path. It appears this signal processing is always performed in the analog domain. At the level of the higher primates, this signal processing occurs at many locations, within and without the brain. In this work, these sites will be defined as engines. Within the central nervous system, these engines are interconnected by groups of signal projection neurons called commissure. In the peripheral nervous system, these same groups of signal projection neurons are given other names like the spinal cord and the optic nerve, etc.

In the peripheral nervous system, recognizing the general direction of signal flow is usually possible, though the signals may follow multiple parallel paths. However, within the central nervous system, the pattern of signal flow rapidly changes to a general architecture described by a star in information theory. In a star architecture, each point of the star can connect directly with every other point. As a result, it becomes very difficult to trace a signal through the system from input to output without a wiring diagram. This situation is reflected in the current state of research into the organization of the human brain. The current research using MRI techniques is beginning to illustrate all of the engines involved in a particular function. However, no specific information concerning the purpose of the processing at any individual engine is provided. This level of detail is still being investigated by what a signaling specialist calls traffic analysis.

1.8.2.1.1 Top level block and schematic diagrams of the human retina

Figure 1.8.2-2 provides a simple global schematic of the signal processing used in the typical animal retina. The generic signal processing function can be addressed from several points of view. The simplest involves treating the retina as a functional part of the brain. The alternative is to treat it as a functional part of the peripheral nervous system that happens to share the cranium with the central nervous system. The latter is more realistic with the identification of the optic nerve (nerve II)between the eyes and the brain as clear support for that view. As noted by Noback in 1967[257],

> "The cranial nerves are the peripheral nerves of the brain. They transmit input to the brain from the special sensors of smell, sight, hearing and taste and from the same types of general sensors as do the peipheral spinal nerves."

The primary task of the retina is to reduce the "data" volume collected by the photoreceptors of the retina by optimally packaging the "information" and passing that information onto other areas of the brain. This implies that the basic function is a converging one. The signal processing system accomplishes this function by operating primarily in two domains, the geometric and the chromatic. Temporal bandwidth limitations on the signal processing function can be interpreted as temporal processing. However, the data shows there is little impact on the temporal characteristics of the signal due to the signal processing circuitry. There is a limitation on the temporal characteristics of the signals as a function of the illumination level. Otherwise, it appears that most temporal processing is accomplished at later stages of signal processing in the brain. The functions are tailored to satisfy different requirements at different locations within the overall field of view of the eye.

There are two distinct neural paths served by the retina, the foveola/PGN/pulvinar pathway and the pathway relying upon the full fovea, the fovea/LGN/occipital lobe pathway. The foveola is located at the point of fixation of the retina and provides maximum acuity information to the brain in support of the Analytical modes (**Section 2.4.2.4)**. The fovea constitutes the remainder of the retina and provides nominal acuity information to the brain in support of the Awareness and Alarm modes (**Section 15.3.1.1**).

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[257]Noback, C. (1967) The Human Nervous System. NY: McGraw-Hill pg 117

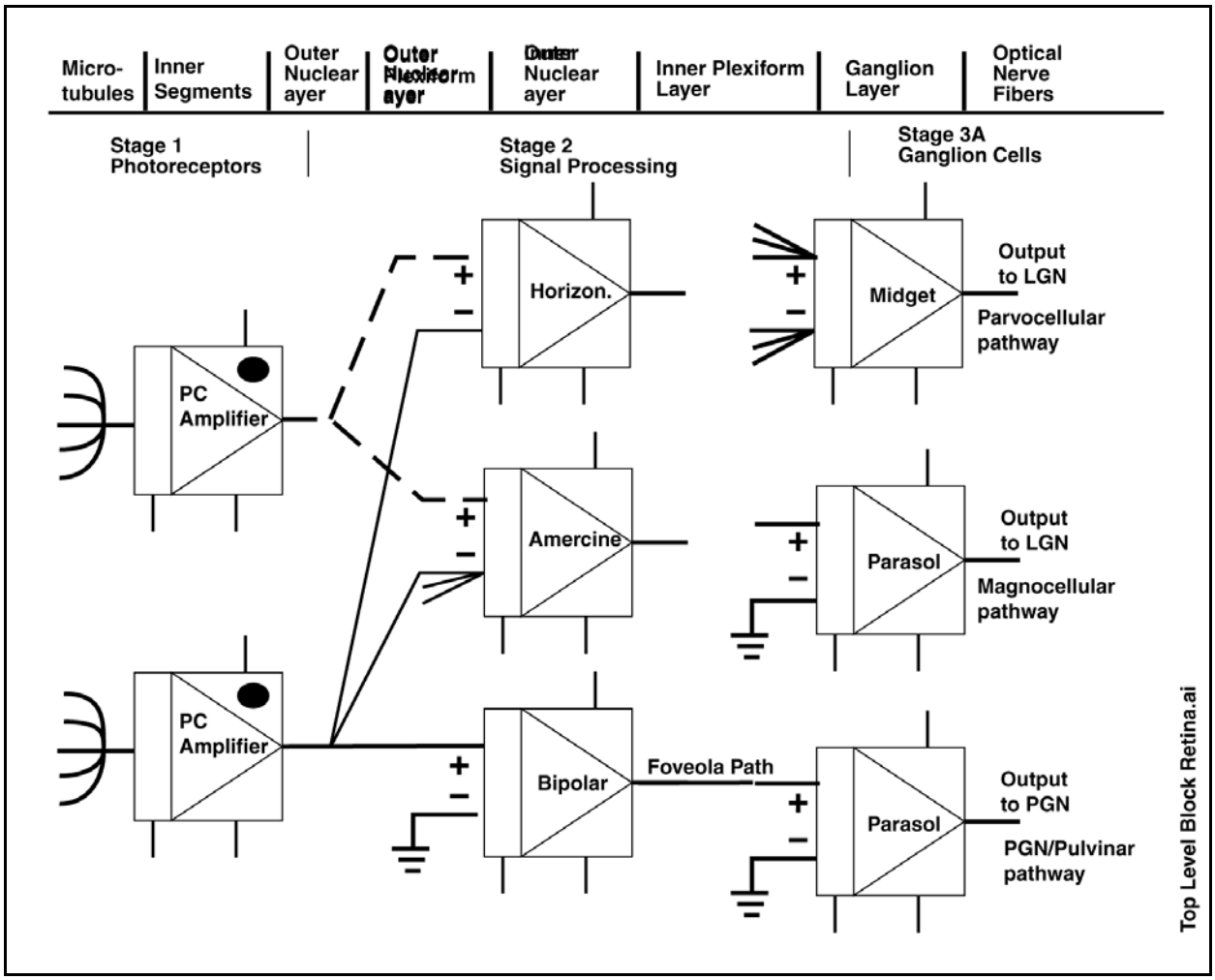

Figure 1.8.2-2 Top level "signal" block diagram of the animal retina. Each of the defined blocks is an active electrolytic neuron processing electronic signals delivered to it via electronic (tight junction) synapses. Beginning with the stage 3A midget and parasol ganglion neurons, the analog signals within the retina are converted to monopolar pulse streams (known colloquially as action potentials) that are propagated electronically in accordance with Maxwell's Laws. The presence of the foveola path is species specific and rare outside the primates and the falconiformes. See text.

The top row of the figure provides the morphological designations for the cross-sectional areas of the retina *away from the foveola*. The left label describes the chalice of microtubules that enclose the discs of the outer segment (not shown) of the photoreceptor neurons. As noted in **Section 4.3.2**, the nuclei of many photoreceptor neurons are physically remote from the inner segment of that neuron. Thus the solid disc shown in the individual photoreceptor neurons is frequently present in the Outer Nuclear Layer rather than associated with the Inner Segment of the neuron.

The Outer Plexiform Layer is the initial signaling matrix involved in packaging the information provided by the photoreceptors. The great complexity of this matrixing varies with distance from the fixation point of the retina. It has not been documented explicitly as of 2019. The matrix provides multiple outputs. The primary output relates to the foveola/PGN/Pulvinar pathway shown along the bottom of the schematic. The bipolar neuron is shown with its inverting input terminal grounded, resulting in a non-inverted output at its axon. Both a horizontal neuron and an amercine neuron are shown with differential inputs. These neurons are used to accept separate outputs of the matrix related to specific chrominance signals, specific summations of photoreceptor signals from large areas of the peripheral retina, and potentially center-surround chrominance data.

The chromatic and geometric data processing loads involve taking (multiple) sums and differences between different

input channels. This load increases with the complexity of the retina. Clearly in the simple eye of *Arthropoda*, containing only a few photoreceptors in one rhabdom, this function is trivial. For *Limulus*, this minimal signal processing can be used to explain the operation of the eccentric cell. In both the compound and complex eyes, the processing becomes more extensive.

The chromatic differences are taken primarily to provide a better definition of the "color" of the sensed light than can be obtained by just assigning a color based on which chromophoric channel exhibits the highest signal level. The horizontal neurons have traditionally been associated with accepting chrominance difference signals.

The geometric channels appear to take sums primarily to provide "alarm" signals to the animal and after that differences to provide detailed definition of the object of interest or concern. These sums and differences are inherently analog in nature. However, if the amplification factors are sufficiently high within the associated neurons, the result will be Boolean, just as in a man-made comparator circuit.

The second row of text in the upper portion of the figure relate to the stages of the block diagram presented in **Section 1.5.1.2.2**. This notation will be used, and expanded, throughout this work as the complexity of the model seeks to emulate the biological situation.

The character of the signal matrixing within the inner plexiform layer has not been explicitly documented beyond its primary role of packaging the information more efficiently. It is known that *chromatic difference signals* from the matrix are used to modulate pulse streams (generally labeled action potentials) stage 3A *midget* ganglion neurons. The output of these neurons are propagated to the LGN over the Parvocellular pathway. It is also known that a *summation of chromatic signals* is converted to a series of pulses describing the *brightness* of the imagery (regardless of its chromatic content) presented to the retina as a function of time. This matrix output is converted to a series of action potentials by the stage 3A parasol ganglion neurons and propogated to the LGN over the Magnocellular pathway.

Stage 2 signal processing within the retina uses neurons operating in an analog or tonic mode. Many authors have provided simple conceptual cartoons of the signal processing circuitry in the retina, including Dowling, Ottoson, and Shephard. These cartoons have not addressed the nature of the devices processing the signals. Closer analysis of the bioelectronics involved leads to a much clearer understanding of the processes, mechanisms and signals involved. The results of this analysis leads to a variety of improved graphics describing the operation of the visual modality in humans (**Chapter 15** and **Chapter 17**).

The output signals created by the ganglion cells and used to transmit information to the brain have not been adequately characterized in the literature. They are usually described as providing pulse type signals where the information is carried by the *frequency* of the pulses. This will be shown to be an oversimplification; *the information is carried in the time delay between the individual pulses*. This type of modulation is called time delay modulation, a form of phase modulation (which also includes frequency modulation). Recognizing the specific type of modulation used (the IRIG code of **Section 14.2.5.2**) allows a much simpler and more precise interpretation of the various refractory intervals frequently defined but not explained in the literature.

Two types of ganglion cells are shown in the figure. The parasol ganglion cells are characterized by output pulses (action potentials) that die out in the absence of illumination. The information they convey is monophasic. The midget ganglion cells are characterized by output pulses that exhibit a nominal temporal spacing in the absence of illumination. The spacing decreases upon illumination of one photoreceptor cell and increases upon illumination of the other cell, following the differential output of the corresponding lateral cell.

The analyses found in **the following chapters** demonstrate that the visual system is designed according to the best sensor design rules. These rules are used in the animal aural system as well and in all high quality man-made detectors. This is true whether they are used for audio, radio, or light detection. The key is to provide the maximum signal gain in the earliest possible stage of the signal processor. To avoid amplifier saturation problems, providing a method of automatic gain control, AGC, early in the signal chain is also necessary. The eye accomplishes these objectives in the first amplifier stage of the photoreceptor cell, which will be called the adaptation stage. It provides very high gain (~3500:1) at the single photon excitation level but essentially unity gain under high photopic illumination conditions. This is accomplished using internal feedback associated with the phenomena of avalanche breakdown. This phenomenon is common in man-made active semiconductor devices.

All of the circuits of the visual system typically operate under large signal, i.e., non-linear conditions.

1.8.2.2 The topology of the neural system architecture

Gouras has provided a drawing of the very simple topology of the neural system of *Arthropoda*[258]. Immediately behind the plane of photoreceptors is a section of the brain, generally labeled the lamina, that provides initial signal processing prior to the signals proceeding to the medulla.

Young has provided a similar drawing of the topology used in *Mollusca*[259]. It is normally very similar to that of *Arthropoda*. The photoreceptors connect directly to the neurons in the optic lobe, sometimes labeled the "deep retina," where they are processed before the signals proceed to a plexiform zone and then to the brain. Except in the unusual case of *Cephalopoda*, there is no structural agility between the eye and the brain. As shown in [**Figure 1.2.1-13**], *C. Octopoda* has achieved a certain amount of agility in one dimension by forming a crossover in the nerve bundle between the eye and the optic lobe.

To achieve adequate agility between the eye and the head, *Chordata* has gone much further. It has moved the signal processing circuitry of the lamina or optic lobe into the retina itself and then added a signal encoding subsystem. This allows a major reduction in the number of individual neurons in the optical bundle (now called the optic nerve). Upon arrival at the brain, these signals must be at least partially decoded before additional signal processing.

1.8.2.2.1 Common nature of signal processing topology among animals

It has only been recently that the biological community as a whole has begun to recognize the existence of analog electrical signal processing (graded potentials) in the ommatidia and more complex eyes. However, confusion still exists in the literature because of the limited experimental results and the use of "floating models."

Contrary to a conclusion drawn by one textbook author based on results drawn superficially from the work of two different sources, and propagated by subsequent textbook authors, only one fundamental sensing mechanism is employed in all animal eyes. The signal polarity found at the output of the photoreceptor cell and rhabdomin are always negative going with illumination. It will be shown that only one type of photoreceptor is used in animal vision when viewed from either a neural or signal generation perspective. All photoreceptors produce a current of electrons as an output signal. This current is converted to a negative going voltage that increases with illumination. The conversion occurs at the pedicle. The data of Laughlin & Hardie[260], the original source, can be used to correct the confusion in the literature over this point. It will be discussed in more detail in **Chapter 12**.

Confusion has also lingered in the psychophysical portion of the visual science community over the notion of inhibition, especially when applied to the neuro-sensory system. Investigators working in the sensor-neuron arena have tended to adopt the terminology of the motor-neuron community. This has been particularly prevalent in that part of the community that has not recognized the presence of analog signals in the neuro-sensory signal paths. Lacking a comprehensive model of the vision process, the situation has now reached the awkward stage.

The idea of inhibition has been used frequently in discussing neurological processes, both in areas of analog processing and in areas of action potential suppression. Inhibition in the psychological community is defined as a conscious or unconscious restraint of a behavioral process, a desire, or an impulse. This definition implies the throttling of one signal by a second without the possibility of the opposite effect, throttling of the second signal by the first. Using this term in motor-neurons where the signals are primarily of the pulse type may be appropriate. It is not the appropriate term in sensory-neurons before the ganglion cells or in cortical signal processing circuits (after projection signal decoding) where the signals are of the analog type.

In biological vision, the signal processing carried out before the generation of an action potential occurs in the analog domain. Two principal types of signal processing paths occur within the retina of biological vision before the generation of the action potential. The first is a straight path between the photoreceptor cells and the ganglion cells. This path does not involve inhibition in the psychological sense. The second is a differencing path that is frequently described as involving lateral inhibition. This differencing path performs an algebraic subtraction between two (or two groups of signals from) nearby neurons. The algebra is carried out in the exponential domain. However, the important point is that the result of this process is a bipolar signal. Both of the bipolar portions of this signal represent a difference between the two input signals. Neither of these portions can be properly described as

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[258]Gouras, P. (1991) Op. Cit. pg. 277

[259]Young, (1962)

[260]Laughlin, S. & Hardie, R. (1978) Common strategies for light adaptation in the peripheral visual systems of fly and dragonfly. *J. Comp. Physiol*. vol. 128, pp 319-340

inhibition for two reasons; the output signal is analog and continuous, and the output signal is symmetrical with respect to both inputs (excepting a possible difference in amplification factors). These facts show that a description such as “ON center, OFF surround” is equivalent to “OFF center, ON surround” if the amplification factors are properly accounted for.

A detailed description of the signaling paths between the photoreceptors and the ganglion cells is extremely difficult because of the complexity in the higher animals. However, the concept was clearly illustrated in a caricature by Franceschini for the fly[261]. A very simple matrix arrangement is found between the individual photoreceptors of the retina and the neurons of the lamina (the first surface of the animals brain). The signal processing within the human retina will be discussed in detail in **Chapter 13.**

Three principle refractory periods are related to the signal path of biological vision. The first involves a transit delay related to excitons in the P/D process. This delay is a variable function of the state of the electrons of the chromophoric material. The second is a delay associated with the time required for a signal to reach a threshold level in the oscillator circuit of the ganglion cell. This delay is also a variable related to the state of the oscillator circuit and to the slope of the signal applied to the ganglion cell. The third refractory period is found in the projection neurons. It is the time between when an action potential arrives at a Node of Ranvier and when a regenerated action potential appears at the input to the next axon segment.

1.8.2.3 The circuits of the neural architecture

Figure 1.8.2-3 shows the fundamental circuit configuration of the visual system. It is drawn to show the four possible spectral absorption bands of the tetrachromatic visual system. However, C only illustrates the two channels, P & Q, found in the visual system of the trichromat. It also places the role of action potentials in proper perspective and defines the electrolytic signaling role of the Nodes of Ranvier. The details related to this figure will be developed in **PART D, Chapters 11 thru 15**.

1.8.2.4 The critical arrangement of the initial signal processing

To achieve the high dynamic range with respect to illumination level required for good terrestrial vision, introducing some method of adaptation to the incident light level is necessary. This process is performed within the photoreceptor cells of the retina. The method used introduces a large degree of negative feedback into the signal path. There is a resistive element and a capacitance associated with this path. As a result, the output of the adaptation amplifier remains nearly constant for signals of any input amplitude and frequencies above zero in the temporal domain. A side effect of this process is that the output of the photoreceptor cell does not respond to slow changes in illumination and it cannot transmit a DC signal representing the absolute level of the input illumination. The retina consists of many individual change detectors, the photoreceptor cells. Therefore, the retina cannot operate as a pixel-based imaging camera. See **Chapter 7**. In the absence of change in the photon flux received by a photoreceptor, no signal is transmitted to the brain. This form of operation is quite satisfactory in sedentary animals occupying a protected niche in the environment. It is also adequate in simple animals who interpret any change in light level as a signal to escape. They react reflexively. However, this capability does not allow the animal to image the world around him. The animal is unable to perceive a stationary scene. Such a capability is quite limiting in both defensive and offensive behavior.

A visual system based only on a change detector is unsatisfactory for the higher animals. This problem has been solved by having the complex eye mounted in an easily rotated ocular. By attaching muscles to the ocular and commanding those muscles, causing the optical line of sight of the eye, relative to the scene, to move continuously is possible. This process modulates the light falling on an individual photoreceptor. The result is a closed loop ocular system that can image a scene. This system is based on a simple open loop photoreceptor that is incapable of imaging a scene on its own. If the tremor induced by the muscles rotating the ocular is suspended, the eye can no longer image a scene. It is only sensitive to motion, or sudden changes in illumination, within its field of view. Tremor is normally a function operating independent of the animals will. However, this is not always the case. The level of the tremor plays an important part in chordate vision, ranging from nearly zero tremor in the frog, to an amplitude of one to two pixels in human. The cat apparently can vary the magnitude of the tremor to optimize its hunting capability.

1.8.2.4.1 The importance of tremor in human vision

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[261]Franceschini, N. (1985) Early processing of colour and motion in a mosaic visual system *Neurosci Res Supplements* vol 2, pp S17

The importance of tremor in human vision is immense although it is seldom discussed in texts because of their predisposition to discuss static situations based initially on morphology. Without the presence of tremor in the oculomotor system, the human eye is blind. Failure to recognize this fact leads to many false premises concerning the visual system. Uttal has provided a recent summary of the effects of stabilization, the artificial removal of the effect of tremor, on the operation of the human eye[262]. He provides a paraphrasing of some conclusions by Ditchburn that are illuminating. Four "types" of transient vision are defined. However, these paraphrases still do not clearly separate the temporal from the spatial aspects of visual images. This subject is addressed in detail in **Chapter 13.**

1.8.2.5 The transition from conduction to propagation

The vast majority of individual animal neurons are analog devices processing electrotonic signals over electrolytic conduits. The basic method of signal transmission over these conduits is by conduction, either ionic or by charge mobility within a conducting medium. Both methods are intrinsically slow compared with conduction over metallic conduits. An additional problem arises when the axon of these neurons is longer than a fraction of a millimeter. Because of their extremely thin axolemma, a considerable amount of capacitance is created per unit length of an axon. This capacitance requires a stronger signal generating source and can lead to significant amplitude loss and phase distortion in any AC signal if transmitted over any significant distance. Animals take several different steps to overcome this problem. Many steps are used simultaneously. A simple solution is to wrap the axons with a high quality dielectric material that is impermeable to the electrolytes of the conduit. The process is described as myelination by the morphologist. This is a bulky, but frequently adequate solution. In other animals, large numbers of neurons are grouped tightly together and surrounded by a single wrapping to achieve the same objective in a package with less passive volume.

The third approach, while not used in many smaller animals[263], leads to the greatest improvement. This approach is to change from the conduction of electrotonic signals within a conduit to the propagation of an electromagnetic wave along the dielectric medium forming the wall of the conduit. This approach offers a velocity of transmission at least several orders of magnitude higher than that of conduction. By adjusting the impedance of various electronic elements within a neuron, the excess capacitance associated with the unmylinated portion of an axon can be used to cause the active device and its circuit to oscillate. This solution converts the phase sensitive electrotonic signal into a much more phase insensitive "action potential." Such a phasic signal can be regenerated easily, without loss of information content, by orthodromic neurons. The resulting system employs action potentials to transmit signals between the signal processing and signal interpretation parts of the neural system. In this approach, the conduit is no longer used as a conductor of quasi-DC signals. Instead it is used as a waveguide for electromagnetic signals.

Since the limitation on the length of a neuron processing an electrotonic signal does not scale with body size, the phyla take different approaches to this problem.

In *Arthropoda*, most of the animals are small to minute. The distance between the photoreceptors and the lamina and medulla are short. Although difficult to verify experimentally, it appears that many members of this phylum do not employ action potentials in the visual system. They rely on very short distances and, where necessary, additional dielectric isolation.

Members of *Mollusca* vary considerably in size and appear to adopt different solutions to the problem based on their size. The larger animals do employ oscillating neurons to generate action potentials. They are also known to employ dielectric wrapping of both individual neurons and groups of neurons. All members of Chordata appear to employ oscillatory neurons to generate action potentials for transmission over the projection pathways of the neural system. These pathways are even found between various individual areas of the brain in the higher animals where they are usually labeled association fibers or commissure depending on the author. A single association fiber is labeled efferent on leaving one area of the brain and afferent on approaching the next area[264]. The use of action potentials within the projection subsystem suffers from one disadvantage. The regeneration process is slow. Whereas, the nominal instantaneous velocity of a neural signal along an axon is 4400 meters/sec, the average velocity between the same point on two segments of axon separated by a regenerator (either a synapse or a Node of Ranvier) is only about 44 meters/sec (See **Chapter 14**). This average velocity is the value usually reported in the neurological literature.

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[262]Uttal, W. (1981) A taxonomy of visual processes. Hillsdale, NJ: Lawrence Erlbaum Associates. pp. 779-790

[263]Laughlin, S. (1981) in Autrum, H. *ed*. Handbook of Sensory Physiology, Volume VII/6B. NY: Springer Verlag. pg 143

[264]Noback, C. (1967) The Human Nervous System. NY: McGraw-Hill pg 233

1.8.2.5.1 The nature of the axon as a cable SHORTEN & REF CHAP 10

Understanding the operation of the axons of signal projection neurons operating as an electromagnetic waveguide has been impeded by the reliance upon a so-called Hermann Cable by the biological community. Hermann's proposal (circa 1905) was not founded on sound electrical engineering principles. It was based on a poor understanding of the cable developed during the age of telegraphy. This was before the age of telephony surfaced the importance of impedance control within the transmission medium to avoid signal dispersal as a function of frequency component. He proposed that the axon was based on a simple transmission line consisting of only resistors and capacitors. This interpretation is not compatible with current transmission line theory. To transmit "pulse" signals separated by a wide time interval, Heaviside showed in 1890 that the concept used in the Hermann Cable was inadequate for wide band signal transmission. He showed that equalizing the shunt and series impedance of the transmission line is a necessity. Such equalization requires the line to include both capacitive and inductive elements. The ideal transmission line matches the product of the series resistance and shunt capacitance to the product of the series inductance and the shunt conductance. Biologists tend to discuss the capacitance per unit length of a neuron in terms of an equivalent flat capacitor. The more appropriate model is a concentric cylindrical capacitor. The concentric model is appropriate to the axon and includes an inherent inductive component. The equations for a concentric cylindrical transmission line are quite simple. Specific values for the capacitance and inductance per unit length of an axon will be discussed in **Chapters 10** and tabulated in **Appendix M**. It will be shown there that a transmission line made up of only capacitors and inductors exhibits a purely resistive input (or driving) impedance. References to a Hermann cable in the biological literature should be discounted.

1.8.2.6 The signal encoding topology of subsequent processing

In the higher animals, including the higher chordates, several levels of signal encoding are employed that are not obvious from the physical architecture of the neural system. Being aware of these manipulations is necessary if the operation of the visual system is to be understood. It is also necessary to remember that the fundamental visual system is based on change detection not imaging. Providing a neural circuit connecting directly from a photoreceptor to a specific location in the brain on a full time basis is not necessary. If a change in the scene is reported to the appropriate part of the brain in a timely manner, the system performance requirements are met. Because the system requirement varies with location within the field of view, different signaling algorithms may be used to support different areas of the retina. These algorithms are implemented in two areas of the neural portion of the retina. Much of the chromatic and polarization oriented signal processing appears to occur in the horizontal cells. These cells are found in the distal part of the inner nuclear layer. Much of the spatial and velocity oriented signal processing are processed by the amercine and other cells in the proximal portion of the inner nuclear layer.

For the photoreceptors of the foveola, the algorithm appears to be a null matrix, e. g., the photoreceptors are supported by individual signal paths to the brain. For photoreceptors outside the foveola, the encoding is so efficient that the signals from individual photoreceptors may be encoded for luminance, chrominance, polarization, and even geometric distance from the point of fixation before being spatially encoded. This can lead to a much higher system efficiency. The signals related to the geometric distance of a photoreceptor from the fixation point appear to also be projected to the brain without further spatial encoding. This allows those signals to be used directly for the rapid repointing of the line of sight in response to danger.

1.8.2.6.1 Diversity encoding

Diversity signal encoding is used to great advantage in the visual systems of the chordates to allow the wide rotational angles associated with the eyes. It is the primary mechanism for allowing the signals from more than 100 million photoreceptors to be transmitted to the brain over an optic nerve supporting only about one million individual neurons.
Diversity encoding involves the coding of large numbers of intermittent signals onto a smaller number of continuously available circuits. The encoding algorithm depends on the instantaneous spatial and temporal characteristics of the individual signals. The tailoring of these characteristics is (was) a major step in the design of the overall visual system.

Although difficult to demonstrate in this introduction, the use of diversity encoding is an obvious necessity to accommodate the high degree of divergence in the signals of the photoreceptors as they enter the inner nuclear layer of the retina. It provides the high degree of convergence in the signals passed from the nuclear layer to the ganglion layer of the retina. This mechanism will be explored more fully in Chapters **11** and **14**.

1.8.2.6.2 Temporal encoding

Time delay plays an important role in the determination of motion in the field of view and in the overall operation of the visual system.

The time delay between signals from nearby, but not necessarily adjacent, photoreceptor cells in the retina plays a large role in the sensing of motion within the visual system. These slight time delays are detected by the horizontal and amercine neurons of the inner neural layer related to the peripheral field of vision and represent motion in the field of view. These signals are transmitted to the midbrain independently of the remaining signals and are frequently used to point the eyes and cause the relevant scene to fall on the foveola.

The photoreceptors of the foveola do not play a large part in the detection of motion within the field of view. Instead, these photoreceptors are connected to the midbrain directly, individually and over wide bandwidth neurons as part of the Precision Optical System, POS. The POS uses these signals to extract the fine detailed information from the scene required by the hunter families of chordates and also the higher primates.

Within the overall visual system, the significant time delay involved in the commissures between various signal processing engines has a major impact on the architecture of the brain. As an example, many critical signal processing paths within the visual system do not pass through the so-called (but archaic name for the) primary visual cortex. Much of the critical processing concerning pointing the eyes is accomplished entirely within the midbrain (except for pointing at the volition of the higher cognitive centers). Similarly, much of the cognitive processing relating to reading and other fine analyses is passed directly from the output of the precision optical system of the midbrain to Area 7 of the cortex without passing through the primary visual cortex. The primary visual cortex is mainly concerned with providing the general context of the scene, not with the mechanisms related to cognition.

1.8.2.6.3 The impact on center-surround and other clinical testing

Reviewing the physical, topographic and encoding architecture of the human visual system leads to the conclusion that center-surround experiments, although relatively easy to implement, are subject to great difficulties in terms of interpretation. To avoid these difficulties, documenting the experimental circumstances to an unprecedented degree is necessary. This is illustrated by many clinically obvious situations. The animal system is designed to apply different algorithms to different zones of the field of view. Later, the data recovered from these algorithms must be merged into a single perception of the field of regard within the brain.

Clearly, there are partitioning lines associated with the algorithms of vision besides those that might be imposed externally as part of center-surround experiments. Data will be presented in **Chapters 15** and **18** to describe these partitions. A circular partition is found between the foveola and the fovea (with a nominal diameter of 1.18 degrees). A second circular partition is found between the fovea and the remainder of the retina (with a nominal diameter of 6.26 degrees). Outside of the fovea, the field of view of each eye is divided into a left and right half by the optic chiasm. A similar division of the upper and lower halves of the merged field of view originates within the prestriated cortex. These partitions are documented within the clinical record.

Because the visual system is a change detector and the retina is an effective signal processing system, care must be practiced in designing center-surround experiments. The chromatic signal sent to the brain does not represent the average color of the area of a center. The chromatic signal represents the average color immediately inside the contour defining the center. In the transition region, the evaluation of this calculated value may be unstable. Because of this feature, center images of near one and six degrees diameter should be avoided in center-surround experiments.

An additional complication is the limited bandwidth of the various channels of the visual system between the retina and the cognitive portion of the system. This can introduce chromatic artifacts as a function of the test intervals used in the test procedure.

1.7.6 Generic brain

The large mammalian brain is the epitomy of brains. They can be compared with those of the coleoids within *Mollusca* as recently illustrated in Barnes, et. al[265]. The human brain can act as an example of a complete animal brain, although in a few respects it is less capable than the brain of specific species. This is the case primarily in the area of processing signals indicative of the polarization of light impinging on the retina. It is also the case for shape and form discrimination. The 2nd lateral matrix of the human retina is not highly developed nor is the portion of the brain supporting this area.

On the other hand, the Precision Optical System (POS) of the human brain, centered on the thalamus, is the key to the superior capability of humans to analyze and recognize fine detail. These capabilities are critical to our ability to

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[265]Barnes, R. Calow, P. & Olive, P (1988) The Invertebrates: A New Synthesis. London: Blackwell Scientific Publications pg 169

read. This system contains elements of the previously identified and labeled auxiliary optical system (AOS).

Except for the foveola, the retina sends signals to the cognitive portion of the brain in a highly encoded "vector" format. While this information may initially show a spatial mapping relevant to the retina (typically in Area 17), this coherence is rapidly lost (in Areas 18-22). The information does not represent a literal image of the field of view. The brain uses the vector information to create a perception of only the important features of a scene.

Signals from the foveola, the very center of the fovea are actually transmitted directly to the perigeniculate nucleus (PGN) of the thalamus without much of the encoding associated with the remainder of the retina. These signals are processed in a very complex two-dimensional associative processor within the PGN and then perceived within the adjacent pulvinar. These two structures are known as the PGN/pulvinar couple. The resulting perceptions are forwarded to the main memory of the brain that forms a saliency map of the surrounding environment. It is this saliency map, which also includes inputs from other sensory channels that is accessed by the higher cognitive centers in order to make decisions.

An unexpected result of this study was the determination that the "primary visual cortex" is less primary than usually thought. By looking at the topology of the brain, a structure known as the thalamic reticular nucleus (TRN) clearly acts very much as a gatekeeper and coordinator of information flow. The frontal lobe is the highest level cognitive center with the parietal lobe acting as a final formatter of information passing to and from the frontal lobe. In this context, the occipital and temporal lobes are primarily concerned with parts of the data reduction tasks associated with the individual sensory systems. It will be shown that not all important visual information passes through the "primary visual cortex." The lateral geniculate nucleus (LGN) and occipital lobe (primary visual cortex) operate as a couple similar to that of the PGN/pulvinar but at lower resolution and capability. In this sense, the LGN/occipital couple is secondary to the PGN/pulvinar couple.

The TRN sends important information from the PGN/pulvinar couple directly to area 7 of the parietal lobe without it passing through area 17 (alias the primary visual cortex).

The details of the above features are developed in detail in **Chapter 15** of this work. **Chapter 15** is organized into two parts to accommodate the rapid growth in knowledge concerning the brain resulting from the introduction of the new magnetic imaging techniques generically called NMR and MRI.

1.7.6.1 Topology and topography of the human brain

Figure 1.8.3-1 is an expanded caricature of the human brain. It includes several features not previously presented in the literature. The most important new feature is the third signal pathway into the brain.

Traditionally, two pathways have been shown connecting the retina to the brain, via the optic nerve and the lateral geniculate nucleus (LGN). The first pathway, passing through the magnocellular layers of the LGN, has been given the generic label of M-pathway. The second pathway, passing through the parvocellular layers of the LGN, has been given the label P-pathway. Unfortunately, the P-pathway is not connected to the parasol ganglia and the M-pathway is not connected to the midget ganglia. The initial letters are reversed in these two cases. To avoid confusion, these pathway labels should be considered archaic. It is suggested that they be replaced by functional designators to avoid confusion as retina related and cortex related studies converge.

It is proposed in this work that, at least for the portions of these two pathways between the retina and the LGN, they be renamed. The new S-pathway (previously

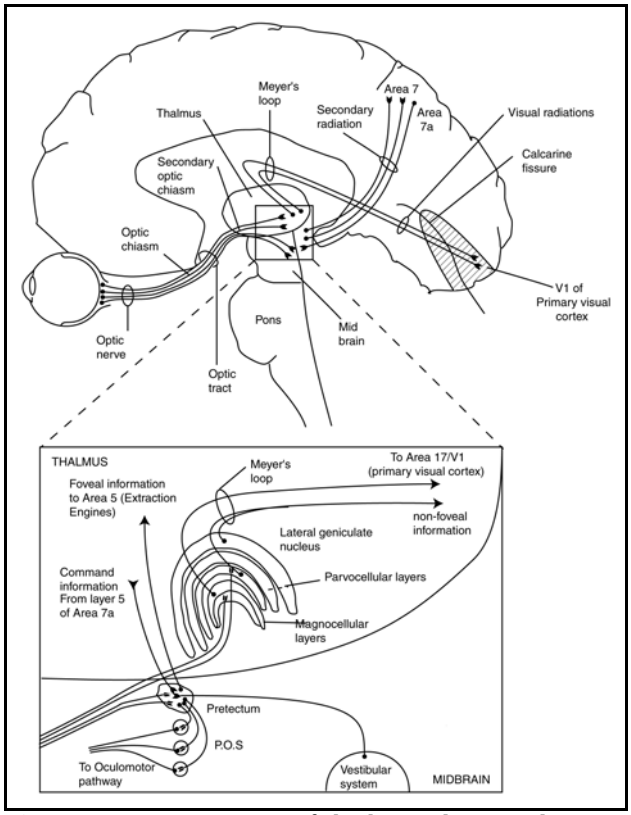

Figure 1.8.3-1 Caricature of the brain showing the main signal paths between the retina and the cortex. Also shown are paths of the auxiliary optical system that control the line of fixation of the eye in inertial space.

labeled the M-pathway) carries luminance signals of the type found in the R-channels, defined earlier, to the primary visual cortex via the magnocellular layers of the LGN. The D-pathway (previously labeled the P-pathway) carries a variety of *difference* signals, from the N-, O-, P-, & Q-channels, from the two lateral matrices of the retina to the primary visual cortex via the parvocellular layers of the LGN. The LGN interleaves many of the above signals, apparently merging the stereo-optic properties of the individual eyes into a single complex data stream. The nature of the signals between the LGN and the cortex is less well understood.

The most important *new feature* in the figure is the third pathway, the retina-pretectum-cortex pathway. This pathway is also labeled the retina-tectum-cortex pathway in some of the literature. Functionally, this pathway carries signals to the cortex that only originate in the foveola. The morphological path is similar to the S-pathway. It is therefore labeled the S'-pathway in this work. This S'-pathway is distinctly different from the S- and D-pathways. It does not pass through the LGN, a region of the thalmus, and it does not go to the primary visual cortex at the posterior of the brain. It passes through the pretectum, a distinctly different area associated with the mid-brain, and goes directly to the higher visual centers, usually labeled V5 as a group. The signals passing along the S' pathway between the retina and the mid-brain are part of the servomechanism that controls the pointing of the eye relative to earth oriented inertial space centered on the location of the animal. The data in this pathway is the most precise and of the highest resolution in the visual system. The Pretectum decodes this information in real time for two purposes. It extracts pointing signals used to interpret the image projected on the foveola. It interprets these images and sends its evaluation of the image, in a highly vectorized form, to the parietal area for transmission to the frontal visual areas and final cognition.

The brain, stage 4 in this work, can be divided conceptually into at least four functional units. They include the initial (sensor related) signal manipulation function, the perceptual function, the later (neuro-musculature) signal manipulation, and the abstract function (including cognition and abstract thought). This work will not address the abstract functions and will only touch on the perceptual functions.

Figure 1.8.3-2 presents an expanded block diagram of the perceptual portion of the cortex and the signal paths supporting it. It also delineates the source of the signals carried by these paths. Our current understanding of the brain is still quite limited. Only about a dozen blocks are shown in the figure of an estimated several hundred similar blocks. However, it is improving rapidly because of the widening availability of the modern techniques of PET, CAT and MRI scanning. These techniques, generally grouped under the title of nuclear imaging (medicine), have provided an expanded source of data that is confirming many previous postulates. The data is also providing a greater degree of spatial accuracy than was ever available before. This precision is exceeding the current numbering systems (dating from the 1900-20's) used to specify areas of the brain.

The current understanding says the perceptual portion of the brain is a highly dispersed series of modular processing sites, which may (and probably do) contain the capacity to store information locally. In this work, these sites will be described as feature extraction engines. Each of these sites, although small in surface area (a few square mm.) still contains at least the processing power associated with a building containing a central telephone exchange. These sites are connected in the most general arrangement, a star network. This allows every engine to communicate directly with every other engine if required.

The concept of a large number of highly interconnected individual feature extraction engines supports the intriguing concept, that there is no centralized, high capability, cognitive center. This concept suggests one of two situations. There is either a master index to all of the data stored in the memories associated with the different feature extraction engines **or** one engine may initiate a query to all other associated engines. Can it be compared with the World Wide Web in this respect?

Although most is known about the S- and D-pathways because of their ease of access to electrophysiologists, multiple investigators have found that the information relating to the image presented to the foveola does not pass through this region. The most important visual

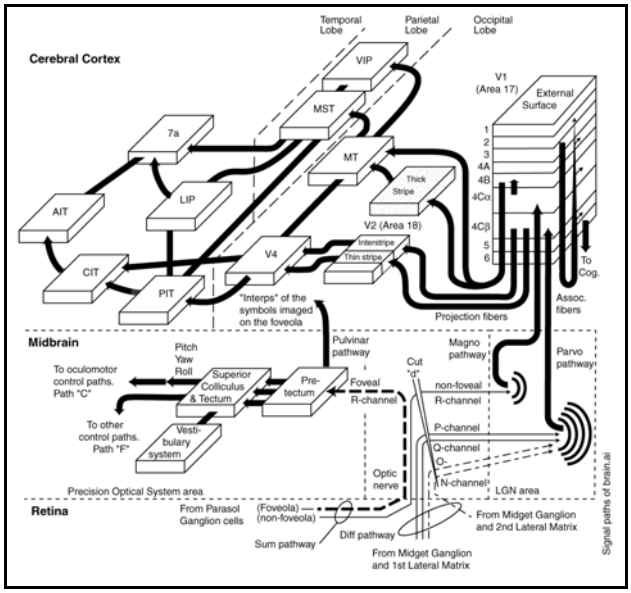

Figure 1.8.3-2 Caricature of the (human) brain. It serves as a prototype of the completely elaborated animal brain although it is less capable in specific areas. The caricature stresses three important pathways between the Thalmus and the cortex and suggests the "primary visual cortex," also known as area V1, is not primary. See Text.

signals relating to the foveola follow paths deeply embedded in the brain and are not easily available for recording. Little if anything is known about their detailed characteristics.

1.7.6.2 Operating modes

This work has not considered a comprehensive search of the brain literature. However, the analyses of the visual system have suggested a variety of new interpretations and baseline parameters for the brain.

1.7.6.2.1 Top level organization

The brain is an extensive two-dimensional sheet of neurons that consists of about six morphologically definable layers or laminates. This sheet has been extensively folded, especially in the higher chordates, to achieve a minimum total volume compatible with other operational and defensive considerations.

The brain is organized as an asynchronous distributed modular system. The modules are grouped according to function. These groups can be described from a variety of perspectives. The most autonomous operations of the brain are centered on the oldest portion of the brain, the hind brain. The next higher level of operations, under at least partial cognitive control, are the responsibility of the midbrain. The new brain, or neocortex, is responsible for a majority of two classes of operation. It is responsible for all cognition and for at least a majority of perception. A caveat applies to the closed loop operation of the servomechanism known as the Precision Optical System (Auxiliary Optical System). This system involves a high degree of perceptual capability in order to interpret the image presented to it.

The neocortex is divided physically into five major physical areas. The frontal lobe is primarily involved in cognitive functions of the highest order. The occipital lobe is concentrated most heavily on the steps leading to visual awareness. It is responsible for receiving and correlating signals from the visual field of view outside of the foveola. To do this effectively, it employs large areas which exhibit a coarse, and not necessarily contiguous, physical correlation to the sensory fields. The temporal lobes perform a similar function for the auditory system. As the information from these lobes is assimilated, it is posted to a saliency map tailored to the animals needs. This map does not exhibit any physical correlation to the visual field of view. In fact, it is probably related to inertial space. The saliency map consists of vectors of unknown format at this time. The parietal lobe is a major crossroads between the sensory lobes described above, the Pretectum, and the frontal lobe.

Each lobe contains a large number of feature extraction engines, estimated in the hundreds to thousands. These engines create the saliency map via an organizational structure that can be well described as a star network. Each engine has the capability of being directly connected to every other engine. Describing these engines explicitly is not possible at this time. To date, only the general nature of the fundamental features interpreted by various areas of the brain has been determined.

The saliency map is directly accessible by a large number of the feature interpretation engines. It appears these engines are also arranged functionally in a star network with a high degree of interconnection between themselves, with the (probably virtual) saliency map, and the feature extraction engines of the occipital and temporal lobes. These feature interpretation engines are the ultimate terminuses of the afferent neurons of the system and the source of the efferent neurons controlling the actions or responses of the animal.

Most of the motor control elements of the brain, except the motor elements of the Precision Optical System, are found on the surface of the parietal lobe of the brain. These areas are situated to receive signals from both the frontal lobe, the occipital lobe and the Pretectum with minimum total time delay compared with the time of any input stimulus.

1.7.6.2.2 Operating modes

The brain operates primarily in the analog signaling mode associated with signal processing. Each engine operates semi-autonomously, receiving and transmitting signals to other engines via the star network of interconnections. Each engine appears to include its own cache memory. When considered in toto, these cache memories may constitute the total memory of the animal. No other area of the brain has been found dedicated exclusively to memory.

All of the processing of signals within each engine is performed by an immense number of unmyelinated neurons. Each neuron contains at least one Activa, and each synapse forms a separate Activa. These neurons appear to be at least partially grouped into separate layers within the brain. The fourth layer from the outer surface appears to be primarily responsible for interconnections with other engines of the brain. In some areas of the brain, the fourth layer has been subdivided into three or more sublayers. Overall, layer 4C appears to be the nominal terminus of

most afferent projection neurons. There is some indication that most interconnections between nearby engines originate from layer two or three and interconnections destined for more remote engines originate from layers five and six. Lund & Boothe have provided detailed morphological studies of these layers[266]. Some of their conclusions may require review based on the three-terminal nature of the neuron.

Actual signal processing appears to employ many analog neurons operating in a high gain mode typical of correlation circuits in similar man-made equipment. Small groups of such circuits are easily interconnected to form latching circuits known as flip-flops. These circuits are typical of circuits employing *external* feedback. The feedback is local to only one or two discreet circuits. Such latches form the basis of volatile memory in analog based man-made circuits. A particularly simple form of latching memory circuit can be made from the same fundamental topology as found in the individual photoreceptor cells of the retina. However, the photoreceptor cells do not incorporate this modification and do not exhibit memory. The circuit is a differential pair with explicit capacitive feedback. Such a circuit can be used for memory of any duration. With this modification, only one neuron is required to provide a discrete memory element.

Because of the size of the elements involved, it is possible that a single synapse may form a complete memory unit. If the Activa of the synapse were of the proper size and is biased appropriately, such an active device could exhibit the Zener effect. Such a device can be considered a Zener diode. Such a diode exhibits a region of negative impedance and can be used as a stand-alone memory element. This would suggest that most of the individual synapses within the brain may be independent memory elements. These synapses could be generated metabolically at any time and then switched electrically, within nanoseconds. Depending on the bias conditions, the switching could result in a permanent change of state for these Zener diodes much like that found in "burning a PROM" for a computer.

The asynchronous nature of the signal processing within individual engines of the brain suggests considerable difficulty in perception because of the availability of important information at different times. Such variability in the assimilation of information accounts for many problems in judiciary proceedings related to eye witnesses and to many illusory and "magic" effects.

1.7.6.2.3 Types of neurons

All of the characterizations of neurons within the brain found in the literature have been based on morphological (cytological) considerations (except for one still classified using the name of the man who described them). They have generally fallen into groups based on size of the arborization field and occasionally on the number of arbors or their similarity to a simple shape such as a pyramid or star[267]. Based on this work, the so-called stellate cells appear to be related to the decoding of signals delivered by projection neurons. These cells are usually described as a subclass of the granular cells. Pyramid cells appear to be projection neurons that perform the encoding of the original signals. As with the retina, horizontal cells appear to support short distance communications laterally within the plane of the neural surface. They are often shown in layer one of the laminate.

> *Using neuron designations based on apparent geometric shape has long outlived its usefullness.* Alternate functional (at the circuit level) designations will be adopted in this work.

Asynchronous switching at nanosecond rates is probably typical for the Activa within individual small neurons. However, the signaling rate is determined by the associated circuit components, particularly the capacitive loading of the axons.

1.7.6.2.4 Interconnections and signal velocities

The brain uses two major classes of interconnections. Over distances of less than two mm., all interconnections are carried out in analog mode between adjacent neurons using "gap junctions," i. e., active electrical interconnection devices. These devices are Activas used as diodes to provide optimal forward coupling, and negligible reverse coupling.

The phase velocity of signals within the myelinated neurons is quite high, averaging 4,400 meters/sec over distances of less than a millimeter. Thus travel times for a nominal myelinated neuron spacing of 10 microns is only 2.3×10^{-9} seconds or 2.3 nanoseconds. For unmyelinated axons, the velocity can be expected to be lower. However, the size

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[266]Lund, J. & Boothe, R. (1985) Interlaminar connections and pyramidal neuron organisation in the visual cortex, area 17, of the macaque monkey. J. Comp. Neur. vol. 159, pp. 305-334

[267]Noback, C. (1967) Op. Cit. figure 16.3

of neurons can be much less than ten microns.

Because of the significance of capacitive loading related to small diameter axons, interconnections extending more than two mm. normally involve signal encoding of the form used in stage 3 of the visual system. The encoding neuron is arranged as an astable, generally monostable, multivibrator. It generates action potentials in response to a stimulus. The axon of this multivibrator is long, *myelinated*, and generally found to incorporate Nodes of Ranvier as signal regenerators. Myelination decreases the capacitive loading related to the axon lemma, several orders of magnitude. The myelination accounts for the white appearance of most of the neural pathways (including commissures) found interconnecting the engines of the brain.

Because of the time required by the action potential generation and regeneration process, the group velocity of signals projected between engines, and between distant locations within the same engine, is low. This velocity, dominated by the time required by the regeneration process, *is typically 44 meters/sec. at 37°C.* To travel a centimeter, the signal requires 23 microseconds.

1.7.6.2.5 Maximum operating frequency–need for cache memory

All of the available data located suggests that the brain exhibits a variety of signals. Action potentials and a variety of other rhythmic and recognizable waveforms are frequently reported. Because extracellular probes are frequently employed in the laboratory, it is common to find these waveforms described as “in the presence of other background signals.” These background signals are normally due to adjacent neuron signaling. They are not normally characterized with respect to their frequency content. Expecting the frequency content of these background signals to be limited by the impedance characteristics of the test configuration and equipment is reasonable.

A typical neuron can achieve a maximum signaling rate of between 500 and 800 Hertz.

This limitation is even true even in the auditory modality where signals within the neural system never emulate acoustic frequencies. They only indicate their presence and amplitude profile. The modality employs neural pathway labeling to designate the acoustic frequency. This labeling is occasionally discussed as “line-labeling.” The method of line-labeling within the biological system has not been discovered.

To overcome the limited signaling rate associated with individual neural paths, the major signaling paths employ groups of individual neurons as fascicules, more commonly labeled “nerves” or “commissure.” Signaling rates over these fascicules are multiplied by the number of neurons, n, present.

In the case of the optic nerve emanating from each human eye, the *maximum* combined signaling rate is on the order of 1.2 million myelinated neuron paths times 500 Hertz or 600 megahertz. This maximum would only be approached during a storm of colored confetti at infinitesimal size filling the field of view.

To support even *average* signaling rates provided by the optic nerves, it is required that the neural engines of the CNS employ equally massive parallel signaling techniques in initial information extraction. The task appears to be divided up between engines of a few million to 40 million neurons each; typically these engines are too small to be individually studied using modern medical imaging technology with voxels on the order of 4 to 8 million neurons.

This would suggest that each engine of the brain can handle a very large number of parallel *analog* operations at a maximum clock rate of above 0.1 gigahertz. By combining the engines of the entire human brain, a data manipulation rate comparable to one hundred or more gigahertz-class man-made microprocessors operating in parallel is obtained.

The ability of the individual engines of the brain to operate at effective clock rates near a gigahertz while the individual interconnection circuits require many milliseconds to transmit the data at signaling rates not exceeding 800 Hertz between engines is a major limitation. It imposes the same problems on these engines as is encountered in similar man-made devices. Modern computer central processing unit, CPU, microcircuits can operate at gigahertz lock rates, but the transmission rates between the CPU and associated computer elements is usually limited to a much lower rate (employing highly parallel signaling rates similar to a commissure).

An overwhelming requirement exists for local cache memory within each engine, and possibly within very localized areas of each engine.

1.9 Summary of major findings

1.9.1 Initial Findings

The work summarized here has involved a significant slice down through the field of anatomy. It started with the gross anatomy of the eye, passed through the arena of histology and then continued to the realm of cytology. It then cut even deeper into the "division of labor" within the individual cell. It finally went into the world of molecular biology/chemistry. As one explores down along this cut, the need to involve related disciplines becomes ever greater. At the cell and molecular biology level, using inputs from a team of researchers from a variety of disciplines to define properly the very experiments to be performed is virtually mandatory. Similarly, a team is usually needed in order to arrive at a defendable theoretical model is necessary. The importance of the need to design experiments more carefully than ever before cannot be overemphasized. To perform an experiment where several important variables are not controlled due to the inadequate background of the investigator is a primary cause of misleading interpretations in the literature. It usually leads to unnecessarily complex explanations of biological processes. *The chemical explanation of the synapse is a prime example.* The Creator seldom wastes time doing things the hard way. It is our job to use the latest scientific knowledge to interpret the correct process at the earliest possible time in our scientific development. This process inevitably runs into conflict with "the old school." However, the pace of scientific advancement cannot and will not take time to reeducate members of the old school; that task will be left to them to perform.

It was expected that differences would surface between this model and some experimental data. In fact, the differences have been few and have generally been explainable by inadequate experimental technique or failure to adequately separate experimental variables. Pains have been taken to highlight these types of problems and their proposed avoidance in future experiments. In other cases, *the definition of the white point in a Chromaticity Diagram* as an example, has been redefined with considerable enlightenment to those in that area of research. Of course, some experimental work has been found to be outside the purview of this model. The value of that work cannot be determined by reference to this model.

Larger differences occur between this model and other models based primarily due to the deductions derived from the experimental data available at the time. These older, less global models have, unfortunately, sometimes become cast in concrete over the span of time. A typical case: since the popularization of the photographic process in the 1900's, the eye has frequently been not only compared with a camera but described as a camera--and the description has seeped into the scientific literature leading to the eye being defined as a camera in a *fait accompli*. Unfortunately, showing that the eye in the higher animals, such as man, is not an imaging camera in a scientific sense is easy. ***It operates fundamentally as a scanner not an imager***; *it emulates an imager* by relying upon a continuous tremor of the oculars.

In a second case, man's natural tendency to divide articles into separate groups, even when the articles belong to a continuum, has caused the division of photoreceptors into two morphological classes, rods and cones. Worse, this morphological description has passed over into the functional area to describe two types of photoreceptors generally based on the high irradiance (photopic) and low irradiance (scotopic) spectral responses of the human eye. Although introduced in historical times, this has become very awkward since no investigator has ever displayed any single organic chromophore with a spectrum that matches the photopic spectral response. Furthermore, no mathematical description of either the photopic or scotopic spectral response derived from fundamental principles has been found in the literature. ***Rods, as a concept, are archaic and must be dropped from any serious discussion of vision.***

In a third case, attempts beginning in the 1930's to describe the molecular level processes occurring in photodetection did not have the knowledge available to consider many physical and chemical processes now known to play a major role in biology. These processes include the concept of a liquid crystal, a transistor, a visual spectral band chromophore, and many others. Lacking these concepts, theories have been proposed over the years that appear very strange to subsequent generations of experimenters, especially those with a multi-disciplinary background.

1.9.2 Discoveries

1. The discovery of the actual chemicals (the Rhodonines) used as the chromophores of vision and their presence in the liquid crystalline state of matter. This discovery replaces the less defined description of the "rhodopsin concept" in vision.

2. The development of the inherent tetrachromatic visual capability of all phyla of animals. The human being among the unfortunate few who are only able use a trichromatic portion of this capability.

3. The discovery of the active electrolytic semiconductor device found in all neurons and crucial to their operation.

4. The discovery that the neurological system in animals employs mechanisms based on *reversible thermodynamic principles.* These mechanisms do not employ a Carnot Cycle, generally do not dissipate heat, and do not conflict with the Second Law of Reversible Thermodynamics.

5. The discovery that the Node of Ranvier is the prototypical synapse. Of all synapses, studying it is the simplest and easiest. Functional synapses, by one name or another occur between neurons as well as within neuron cell bodies and at intervals along myelinated axons.

6. The discovery of the complete Excitation/De-excitation Equation, E/D Equation, that appears to be common to all of the first stage sensory neurons of the biological neural systems.

7. The discovery that basically all of the neural elements of the biological system exist in the liquid-crystalline state of matter.

8. The discovery of the complexity of the unique energy state of the semiconductor known as liquid-crystalline water.

Although this work was planned to present the details of the operation of any eye, it inevitably expanded into the area of the neuron. One result was unexpected and revolutionary. This was the definition of the active electrolytic semiconductor device in every neuron, the Activa. The excessively narrow view taken by many researchers in neuroscience is highlighted in this work by the definition of this "biological transistor." Besides occurring internally in every neuron, it forms the very heart of every synapse. *Katz warned about an excessively narrow view in 1983 when a major symposium disallowed discussion of the matter of electronic synapses*[268].

The description of the Activa will undoubtedly be fought by a large portion of the neuroscience community. However, the absolute congruence between the physical processes underlying the active portions of a neuron and a semiconductor-based transistor are overwhelming. Recognizing this congruence and then defining a biological transistor based on the same basic principles completely negates the need for uncontrolled variable resistors as used in so many simple models found in the recent, and current, vision literature. Recognizing the underlying transistor in the operation of a neuron, provides a precise physical and mathematical description of these "variable resistors."

The Activa is a three-terminal device, as opposed to the longstanding assumption that the neuron involves a two-terminal circuit. The three-terminal configuraton offers a great deal more flexibility than a two-terminal device.

An additional startling discovery is the fact that the circuitry of neurons uses electrolytic resistances that do not dissipate significant electrical power. These resistances are characterized as the forward impedance of a semiconductor diode.

This work has defined the Matrix Theory of signaling in biological vision. This Matrix Theory, that applies to all visual situations, replaces the earlier and more limited Zone Theory. The Zone Theory only applies to color vision at a fixed light level. The Matrix Theory forms the foundation for both the Young-Helmholtz and the Hering theories of color vision. It also accounts for both the adaptation characteristics of the eye and the spatial tuning found in some eyes. The Matrix Theory provides the mathematical foundation for the photopic, scotopic and mesotopic luminous efficiency functions.

In reviewing the literature on signaling, several points become clear. Very little examination of the theoretical requirements of the signaling process has appeared. Very little analysis has appeared of how the required signaling might be carried out in a biologically realizable way. This is understandable because of the small amount of serious, mathematically based, modeling of both the overall and individual fragments of the visual process that has occurred. This work introduces alternate theories of the signaling process, which are biologically realizable, have been recognized in the ***in situ*** experimental literature, provide signals that can be treated mathematically, and provide insight into the higher levels of processing.

A very prominent shortcoming in much of the psychophysical and bio-electronic probing experiments related to the eye has been the failure to separate what is generally called the large signal and small signal situations when planning the experiments. Electronics engineers long ago encountered the need to address this situation. The same situation must be addressed in vision. Eyes were (apparently) designed for optimum performance under low contrast image conditions applied over a very wide dynamic range related to the diurnal illumination level. Other than when observing a lightning flash, a tongue of flame from a fire or man-made illuminations, the normal eye does not usually encounter a "large" signal input, i. e. a very high contrast input. As will be seen later in this work, the eye

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[268]Katz, B. Sir (1983) Synapses, ed. by Cottrell, G. & Usherwood, P. London: Blackie & Son pg. 1

operates in a generally linear mode in the presence of small signal inputs and in a drastically nonlinear mode when pushed to perform at high contrast in the laboratory.

DeVoe[269] took the position: "It is, in general, a dubious proposition to study the properties of a nonlinear system in terms of its small-signal, linear behavior, in as much as the linear behavior is more apt to be a special case of the nonlinear behavior than vice-versa." He was too generous in this statement; the small signal (quasi-linear) case is *always* a special case of the large signal, nonlinear case. It is the duty of any investigator to make clear the operating mode he is experimenting in, and not to attempt to apply his data to situations involving a different operating mode. If he wishes to relate the data to a different mode, he must highlight the required corrections to the data.

The conceptual development of this model has involved a process similar to teasing apart and describing in detail the individual threads of an artistically woven fabric. The result is a theory with no obvious starting point or ending. The order of presentation of the model and its mathematical parallel is therefore arbitrary. For convenience, the presentation will be similar to that in most compendia on the subject, except an early section describing the overall model, and its major subdivisions, in generalities.

The author has sought to tailor, but not cut without discussion, the whole cloth of the fragmentary models of the vision process found in the literature. It appears this process has led to a spectacular expansion of knowledge about the overall visual process and to the exact mathematical description of the individual processes involved. Often, the equations agree with the literature to an accuracy of one part in 300-- 0.3%. This expansion has also led to the definition of new, and more precise experiments needed to extend the knowledge base even further.

1.9.3 Realizations

Linearity is not a valid concept related to the visual process.

Additivity as a concept derived from Linearity, is not applicable to the visual transduction process. However, a more general concept of summing and differencing is found within the neural circuitry.

Superposition, based primarily on Linearity, is not applicable to the visual process, even under small signal conditions when investigating color perception.

The photodetection (transduction) process involves a mixture of linear and square law processes.

The high degree of negative internal feedback within the outer segments of the photoreceptor neurons allows the entire remainder of the visual system to operate in a mode defined by a fixed amplitude range that must be considered highly nonlinear.

> **The catastrophic failure of the brain and neural system can be caused in two distinct ways.** A lack of oxygen leads to significant damage or death to the homeostatic portions of the brain cells. A lack of glycogen leads to significant interference with or the death of the neural (signaling) portions of the brain cells.

The visual system can be placed under maximum stress in two ways.

1. A large area of uniform retinal illumination at hypertopic levels can cause a significant deficit in the available supplies of the neuro-facilitator glutamate within the Inter Photoreceptor Matrix(also known as the outer segment layer) and/or in the inner segment layer of the retina. This situation generally causes pain associated with the eyes.

> This condition corresponds to the commonly observed condition of snow-blindness caused by looking across an expanse of solar illuminated snow for an extended period without taking precautions.

2. Exposure of a large area of the retina to a rapidly changing pattern with a elemental pitch matching the diameter of the photoreceptor cells can place a major load on the signal processing (stage 2 and stage 4) circuits of the visual system.. This condition can cause a sensation of pain in the eyes and rapidly result in a feeling of mental fatigue.

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[269]DeVoe, R. (1965) A non-linear model of sensory adaptation in the eye of the wolf spider. in Bernhard, C., editor. The functional organization of the compound eye. NY: Pergamon Press (Symposium Publ. Division.

This condition is commonly observed in the fall of the year in forests of aspen as their leaves change color. The aspen leaves are attached to the tree by a unique swivel joint. As a result, the apparent brightness of the individual leaf can change dramatically, at a rate of 10-60 times per second, in the presence of a light breeze. When viewed from the appropriate distance, an ensemble of such leaves, in the presence of a light wind, can cause a significant neural load on the visual system.

1.9.4 Tools

The overall model also calls for the modification of certain "tools" used in the visual science community to provide more precise answers to many practical applications. An example is a proposed update to the well known CIE Chromaticity Diagram (1931, 2° Standard Observer) of the human visual spectrum (which has been reviewed periodically but only within the framework of a ponderous bureaucratic process). The current CIE chart implies that the visual photoreceptors have a peak sensitivity near the corners of the triangle, which is misleading. Similarly, the C.I.E. Photopic (1931) and Scotopic (1951) functions are highly smoothed curves because of averaging over several coordinates; a 2° field of view, data from multiple investigators, and roughly 30-50 nm spectral bandwidths used to obtain the original data. Judd proposed a modification to the C.I.E. Photopic (1931) function in 1951 that more accurately portrayed the sensitivity in the blue portion of the spectrum. This function has achieved *de facto* acceptance in the scientific community although the C.I.E. chose not to adopt it formally for commercial reasons.

Interestingly, Daumer (discussed in Krantz 1975) working with honeybees created a "CIE Diagram for Honeybees" which more precisely reflects the peak spectral responses of the honeybee and many other insects who respond to both ultraviolet and some (human) visual wavelengths. More recently in working with tetrachromatic vision in fish, Neumeyer & Arnold developed a four cornered, (three-dimensional) “CIE Diagram” for that situation. Data from the 1970’s and later frequently use spectral filters with bandwidths from one to 10 nm resulting in much finer data than available in the 1950’s and earlier. Because of the great importance of the CIE (1931) diagram to the entire dye chemistry industry and its client industries, millinery, paints, pigments, etc. , proposing any change in this diagram is irrational. Recognizing the limitations of this diagram and then creating other distinct diagrams is much more productive. It is proposed to create a separate “Chromaticity Diagram for Human Vision (2016),” or “Chromaticity Diagram for Research (2016).” This new diagram would avoid the difficulties inherent in the general diagram (1931/1951) and would be available for researchers to use as a more accurate foundation for their work.

Furthermore, it must be stressed here that most of the material resulting from the CIE deliberations of more than 60 years ago were designed to produce *practical “engineering” guidelines* based on averaging data from multiple investigators. The use of the term engineering in the biosciences hardly equated with the term as used in the engineering community until at least the 1990's.

To aid the resolution of terminology problems, a Glossary has been provided as part of this work. As a starting point, the author insists as Lewis Carroll[270] wrote, "‘When I use a word,’ Humpty Dumpty said in rather a scornful tone, ‘it means just what I choose it to mean--neither more nor less.’" This is particularly important in the visual field where so many words have been used to relate to a different literal picture or have become clichés. An effort will be made here to provide a global and consistent picture.

1.9.5 Summary of concepts and phenomenon based on this work

Because this model is based on many different concepts than other similar work--and on these concepts as a group--the Appendices contain a summary of the concepts used in this work. Some of these concepts are given below in very brief form:

+ **Note**, the following comments focus primarily on the human eye but apply generally to all eyes in the animal kingdom. Sometimes, specific caveats are mentioned in the comments. In other cases, the caveats will be explored in the main work.

1. The eye is blind in the absence of relative motion between the retina and the image presented by the optical system.

2. The photoreceptors of the eye operate as (instantaneous) change detectors and not as integrating devices (which

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[270]Carroll, L. (1872) Through the Looking Glass. Chap. 6. London:

typically involve an integration time interval) such as film and television cameras.

3. Photoreceptors operating as change detectors are not susceptible to saturation by the high flux density of thermally generated photons within the eye cavity.

4. Human color vision involves four types of photoreceptors having different specific spectral absorption bands. The operation of the ultra-violet photoreceptors, as in all large animals, is hindered by the transmissivity of the lens.

5. The spectral absorption bands of the eye are not broadband as usually found in metal or semi-metallic detectors involving the conduction band. The bands are narrow and due to resonance absorption found only in the organic chemistry field.

6. Resonance absorption is a unique property of organic dyes of the conjugated carbon family containing two (as a minimum) organic auxochromes per molecule.

7. Resonance absorption is most important when the organic dye is in a highly aggregated state, preferably deposited on a substrate, where it exhibits "conduction" of electrons (called excitons) throughout the body of this "liquid crystalline substance."

8. Following the absorption of one or more photons by the photoreceptors, the energy is transferred to the nervous system, subject to a minimum energy threshold, similar to that found in silver halide photo-chemistry.

9. The absorbed energy from multiple individual photons can be summed to reach the energy threshold of the nervous system.

10. The first level of signal processing in the eye, following the above thresholding, involves unique nerve cells operating in an analog mode.

11. The signal processing in the eye is generally based on a logarithmic summation and not linear summation.

12. The overall spectral performance of the eye at high light levels, the so-called photopic response is given exactly by the logarithmic summation of the signals from the three chromophoric channels.

13. Due to the unique properties of the eye in detection, thresholding and logarithmic summation, the low light level sensitivity, the so-called scotopic response, is also given exactly by the logarithmic summation of the signals from the same three chromophoric channels. The difference between the scotopic and photopic responses is due entirely to the relative loss in signal current in the L-channel. No separate photoreceptor type is found in the eye exhibiting a scotopic response.

14. There are three recognizable peaks and two inflection points in the spectral response of the human eye. The three peaks are related directly to absorption by the individual chromophores, at 437, 532 and 625 nm. The inflection points are located at 495 nm and 580 nm, and are perceived by the animal following retinal (stage 2) computation related to the brightness (R– or magnocellular) channel.

15. The temporal response of the eye can be completely described mathematically, for both "bright" adaptation and dark adaptation, after considering the "state" of the eye. This includes the state of excitation of the molecules in the outer segment of the eye. It also includes the metabolic state of the remainder of the eye that provides energy to the neural system of the eye. The metabolic system varies in performance over the surface of the retina. This variation accounts for most of the difference in temporal performance reported for different zones of the eye.

16. Most investigators in the past have not delineated the differences in the optical system of the eye found between the aquatic animal world and the terrestrial animal world. Proper understanding of the performance of the terrestrial eye requires that the eye be recognized as an "immersion type" optical system, i. e. the space between the lens-group and the image is filled with a medium with a different index of refraction than in the space between the lens-group and the object. Showing an off axis optical ray as a straight line between the object and its image on the retina is not correct.

17. The eye exhibits a number or special features in animals who operate in both aquatic and terrestrial environments.

18. The eye of humans, a number of other terestrial animals incorporate a field lens formed by the shape of the inner limiting membrane forming a lens identified as the foveal pit. In conjunction with the main optical group, a Galilean telescope is formed in the eye providing higher acuity for the photoreceptors of the foveola (1.2° diameter area of the fovea centered on the line of fixation.

1.9.5.1 Brief Table of Chordate Eyes

It is remarkably difficult to find data on the dimensions of chordate eyes in the academic literature.

Figure 1.9.5-1 presents a figure from Osorio, Vorobyev & Jacobs in Kremers, 2005. The values are only provided for approximate comparisons before exploring these parameters in greater detail in the following chapters. They should not be cited due to the caveats quoted in the caption.

Species	Eye size/PND* (mm)	Ret magn. μm/deg	Peak cone density/ 10^3 mm^2	Theoretical resolution cpd	Reference
Microcebus murinus	9.65/5.00	87	8	4.2	Dkhissi-Benyahya *et al.*, 2001
Galago sp.	18.26/9.65	165	8.5	8.2	Dkhissi-Benyahya *et al.*, 2001
Aotus sp.	–	200	16.3	13.7	Dkhissi-Benyahya *et al.*, 2001
Tarsier spectrum	15/–	150*	50	18	Hendrickson *et al.*, 2000
Human	24/16.7	280	199	67	Curcio *et al.*, 1987, 1990
Macaca fascicularis	17.12/12.17	211	100	36	Lapuerta and Schein, 1995
Callithrix jacchus	10.9/7.63	128	190	30	Troilo *et al.*, 1993
Cebus apella	18.4/11.3	197	169	44	Andrade da Costa and Hokoc, 2000

*Estimate PND, posterior nodal distance.

Figure 1.9.5-1 Brief table of chordate eyes. "The cited publications listed give details of retinal topography outside the area centralis." "Resolution is estimated from the cone density and the optical magnification of the ey according to the formulae given by Snyder & Miller (1977); this is an upper limit." Without considering the foveola (area centralis), these values can only be considered estimates. The PND values given may not recognize the index of refraction of the vitreous humor in these immersed optical systems. In the case of the human, the Ret magntude and peak cone density do not reflect the presence of the field lens and increased focal length of the optical system serving the foveola. From Kremers, 2005.

It appears that the photoreceptors of the chordate eye have a minimum diameter on the order of two microns regardless of the focal length of the optical system. This is due to the requirement that the outer segment of the photoreceptors act as a waveguide at all spectral wavelengths of interest to the species in order to achieve maximum absorption efficiency (**Section 4.3.4.2.1** & **Section 17.3.7**). The L-channel sensitivity will be the first to suffer if lower diameter outer segments are employed.

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