Excerpts from

PROCESSES IN ANIMAL VISION:

including,

ELECTROCHEMISTRY OF THE NEURON

This material is excerpted from the full β-version of the text. The final printed version will be more concise due to further editing and economical constraints.

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PART E

OVERALL PERFORMANCE of the VISUAL SYSTEM

This PART concludes the main body of this work. It includes a chapter summarizing the performance of the visual system in animals from a mathematical perspective, with an initial focus on the human. The following chapter summarizes the same performance graphically. The third chapter reviews both clinical and anecdotal abnormal color vision in humans. The final chapter provides a comparison between this theory applicable to vision in all animals with alternative theories that are primarily limited to humans.

Three major findings of this work appear in this PART and should not be overlooked.

+ **First, the architecture of human vision, like that of most (if not all) chordates is tetrachromatic.** The overall performance of the human is restricted by the absorption of his lens. Because of this blockage, humans are best described as blocked tetrachromats as opposed to trichromats.

+ **Contrary to the baseline assumed by the CIE, and derived from Young, the visual system is not based on additive color.** While the actual chromatic processing in vision is closer to the subtractive color suggested by Hering, **the subtractive color concept does not provide an adequate baseline either**. Chromatic processing in biological vision is based on a slightly more complex method that can be described most simply as <u>differential color</u>. A more complete label would be <u>multichannel, orthogonal differential color</u>. The system takes the difference in signal intensity between pairs of chrominance channels determined by the spectral absorption of the chromophores. It then processes these differences as if they were orthogonal to each other. In interpreting the result, it defines white as the achromatic point where the signal value in all of these channels is zero.

+ The experiments performed in the 1950's by Wald did not successfully isolate the L-channel receptors of human vision. He incorrectly determined this peak to occur near 575 nm (the actual location of the Brezold-Brucke Peak). **The actual L-channel spectral peak is at 625 nm in human vision.** This can easily be demonstrated psychophysically by repeating the experiments of Wald using brighter sources to achieve more complete differential adaptation.

+ With the elucidation of the role of the paleo-cortex in the human visual system, it is now possible to delineate how the human species can read. It is also possible to describe why other species cannot. This shows that the lower primates can no longer be used as a model in leading edge research on the human visual system. The visual system of the *homo sapien*, is significantly different from all other primates.

Virtually no competing theories recognize the fundamental tetrachromatic foundation for animal vision. They are essentially all focused on the human and assume trichromacy instead of the more appropriate blocked tetrachromacy. **While trichromacy will occupy a place in lower education for a long time, trichromatic theory has no place in the graduate educational environment and serious research**.

This last chapter cannot be exhaustive. The author hopes the body of this work speaks for itself in the above areas.

PREFACE TO THIS PART

Before beginning **PART E**, it is appropriate to make a series of summary remarks concerning matters that will not appear explicitly in the following material.

This work has deviated into several areas outside the original plan because of the need to understand the impact of these fields on the overall process of animal vision. One of the most significant was in neurology. The purpose was not to disturb current hypotheses. However, many hypotheses were uncovered that did not follow from the original experimental work. Some of these hypotheses were merely based on narrow foundations that did not recognize the possible alternatives. As a result, it was necessary to reinterpret the experimental data, seek the active device that was responsible for this performance, and finally to define a new biologically based semiconductor device, the Activa, consistent with physical chemistry and the experimental data. The definition of this device led to the startling discovery of the fact that every neural connection is fundamentally an electronic one occurring at a "gap junction" and that all other synapse activity is involved in supporting the electrical needs of the active devices. Adding to the amazement was the recognition that the gap junction itself is an active device. Only time will permit the neurological community to review and accept these hypotheses. However, the understanding of the visual process cannot wait. It has been shown that the basic active mechanism associated with all neurons is an analog device, the Activa. This device can be easily configured to provide analog amplification and inversion within the signal processing class of neurons. It can equally easily be configured, using elements external to itself but within the neuron and its environment, to regenerate pulse signals that are known as action potentials within neurological community. These action potentials are associated primarily with the signal projection class of neurons. Finally, the Activa supports two hybrid tasks. The first is encoding analog signals into a pulse train of action potentials. This is complemented by the task of decoding of those action potential signals at the receiving point, if required. This decoding can provide a graded response to a signal consisting of a pulse stream.

The author has known for more than thirty years that the photochemistry of Retinal & the putative Rhodopsin were not the photochemistry of animal vision. However, the proper venue was not available to successfully challenge this bedrock of the visual science community. This venue has now been found. It is large enough to allow both a concise but complete exposition of the Rhodonine photochemistry of vision. It is also large enough to include a description of the shortfalls of the chromogen Retinal, and the inability of these shortfalls to be overcome through a union with Opsin. It is hoped that this has been accomplished in the previous Chapters.

The more recent ion-pore hypothesis and its associated ion cascade hypothesis, related to signal translation following transduction, are only distractions in terms of the development of a larger comprehensive theory of the visual process in animals. The author cannot give any weight to these hypotheses until someone demonstrates unequivocally that there is a biological cell membrane surrounding the Outer Segment of the photoreceptor cell. The chemical materials forming the basis for these theories are crucial to the process of vision, but they are not related to the signaling function. They are bio-energetic sources used to power the electronically based signaling neurons. They accomplish this via the glutamate cycle found in studies of metabolism.

On one occasion, the author was criticized for not incorporating a discussion of a chemical known allegorically as Transducin. The model presented in this work does not exhibit a need for a material with properties associated with the ephemeral Transducin. Until a specific chemical formula is established for Transducin, or recognizing that difficulty if the material is used catalytically, the formula for the reaction it might be specifically supporting, there appears to be no reason to discuss Transducin further.

CURRENT C.I.E. STANDARDS

In lieu of a full chapter devoted to the C.I.E. Luminosity Functions and the Chromaticity Diagrams, only three paragraphs will be presented here. The original plan was to provide a mathematical road map showing how the C.I.E. Luminosity functions and Chromaticity diagrams could be developed beginning from basic principles. As the basic principles were organized into a framework, it became clear that these presentations could not be rationalized to a mathematical foundation. Boynton[1] focused quite specifically on this fact in his review of the development of the C.I.E. Chromaticity Diagram. For two pages, he insisted on using the triple bar equality sign to stress: "The plus sign is borrowed to indicate colorimetric addition by superposition of lights; the symbol "≡ " is deliberately used to make it clear that an experimental match is implied, rather than a mathematical equality." Unfortunately, he then reverts to a conventional equal sign in the rest of his exposition. Many others have apparently taken the use of the triple bar equality to indicate a mathematical identity, just the opposite of Boynton's intent.

[1]Boynton, R. (1979) Human Color Vision. NY: Holt, Rinehart & Winston pp.390-405 *also in* Woodworth and Schlosberg's Experimental Psychology, 3rd. (1971) NY: Holt Rinehart & Winston pp. 352-358

There are three fundamental, and one technical, problems with the foundation under the C.I.E. work in this area. The first three are interrelated.

The **first problem** relates to the extension of the Young-Helmholtz proposition that three spectral channels were employed in human vision to two related corollaries based on the hypothesis that the visual process can be explained using linear additive color mixing principles in object (stimuli) space. The fundamental architecture, and the resulting signal manipulations used in vision are not compatible with or explainable by additive color mixing principles.

The first corollary has become widely accepted. It requires the mixing of three individual colored lights to match a given light in stimuli space using the human eye as a matching device (or null detector). The second corollary says that, in some sense, the light to be matched must occupy a space on the Standard Chromaticity Diagram that is internal to the perimeter formed by connecting the x,y (or u,v) coordinates of the three individual lights. As shown in Chapter 17, these corollaries do not conform to reality.

This theory explains how it only requires two properly selected spectral lights for the perception by the human of any "color" including white under a constant state of adaptation. If the two lights are narrowband, they can result in the perception of any narrowband color in two-dimensional color space. If the color to be matched is represented by a broadband color (finite spectral emittance in at least one dimension), the two spectral colors must have appropriate wideband spectrums. The broadband spectrums need not be identical or proportional to that of the light to me matched since an integrating process is involved. This integration explains the phenomenon of metamerism in vision. The color mixing aspect of the conventional trichromatic theory is not sufficiently precise. A third light is only required when the test lights are not spectral in character.

The signal manipulation architecture of the visual system typically employs three chromophores of relatively broad band spectral response. Because of their broad band nature and the differencing employed, it is not necessary for the chromophores to be located at the corners of the chromatic range in stimuli space. As long as the difference signals are monotonic, the stimuli can have any spectral content (in the stimuli space represented by the P,Q coordinates in perceptual space) that results in a difference signal that is above the intensity threshold levels of the visual system. The color matching capability of the eye extends from a quite specific limit at 400 nm. to a less defined long wavelength limit beyond 655 nm.

Boynton hinted at the **second problem**. The basic "Color Equation," expressed in linear algebraic space and used in the development of the C.I.E. material, <u>is not the correct equation of color vision</u>. The correct color equation is written in logarithmic algebraic space. In this space, the equality sign holds absolutely. However, the relevant mathematics involves subtractive principles. With these two changes of underlying principles, the "color matching functions" of human vision become real. This is true whether they are used to calculate tristimulus values based on an equal energy spectrum or an equal flux spectrum. With a real set of color matching functions in RGB space, there is no need to create a synthetic XYZ space where all of the spectral components have real values. **The third problem** involves the assumption of a trilateral, as opposed to an orthogonal, relationship between the colors perceived by a human. As has been shown in developing the model and will be shown in **Chapters 16 & 17**, all animals calculate color difference signals. The human calculates the color difference pairs, S- minus M- and L- minus M- (justification given in the following chapters). These calculations are independent and are most appropriately presented in orthogonal space. The result is a fundamentally different and new Chromaticity Diagram. The author is pleased to note that the new diagram satisfies a number of long sought needs. Fundamentally, it provides a true representation of the perceived chromatic performance of the eye that can be projected into object (or stimulus) space. It also provides a unifying explanation for the theories of Young and of Hering, and the ellipses of MacAdam appear as circles on the new Diagram, as they should from a philosophical system design point of view.

The primary technical problem with the C.I.E. material is that it was compiled from the work of a group of laboratories employing different quality instrumentation available in the 1920 time period. The compilation was by simple averaging as a function of wavelength, and some "Kentucky windage" as so eloquently described by one of the participants[2]. The material came under almost instant criticism from the Chairman of the committee submitting the Standard[3]. The result was an overly smoothed set of luminosity functions that are only suitable for photometric engineering purposes, and definitely not suitable for the purpose of vision research.

The C.I.E has not considered the ultraviolet sensitivity of the human retina or the eye in its deliberations. Its various standards are not adequate for research purposes.

CONTENT

Chapter 16, The Equations of Vision and their confirmation, focuses on the development of the equations describing the overall performance of one or more stages of the visual system without concern for the performance of the overall system which is addressed in **Chapter 17.** To achieve this, the detailed mathematical description of many of the individual circuits of the visual system are developed. The emphasis is on the understanding of individual performance parameters, as measured in the laboratory, in terms of internal functional parameters associated with an individual circuit up to several stages of the overall system. The mathematics related to the most prominent psycho-physiological and electro-physiological experiments are reviewed in detail.

No curve fitting using series expansions, or any other approximation techniques, are used in Chapter 16.

Chapter 17, Performance descriptors of Vision, is a graphic summary that brings together all of the preceding work. It begins with an overview of concepts and terminology, some of which has been presented earlier, and reviews the historical descriptors of vision. It then reviews in detail the luminance, chrominance, combined luminance and chrominance, temporal, and spatial characteristics of the visual system (with an emphasis on the human).

This chapter includes the description of the performance of both the retina and the complete eye in the ultraviolet region. The analysis shows that the so-called trichromatic eye is based on a tetrachromatic retina. It is the lens of the eye in humans, and other large chordates, that limits the performance of the visual system to the trichromatic range. Hence, the human eye and visual systems are more completely described as a degenerate tetrachromatic system.

The luminance sections provide rigorous descriptors of the luminosity function as a function of intensity and new luminous efficiency functions as a function of wavelength under both photopic and scotopic conditions. It also describes the continually varying function found in the intermediate mesotopic condition. It concludes with the theoretical luminance threshold function. All of these functions are shown to match the experimental data very closely or to devolve to the experimental condition through smoothing to account for the instrumentation used. In particular, the C.I.E Luminous Efficiency Functions are shown to be instrumentation dependent to a much greater degree than generally known.

The chrominance sections develop the chrominance discrimination function under a variety of parametric conditions. It develops a new Chromaticity Diagram for Research that is perception based but can be extended into object (stimulus) space. A series of auxiliary axes are provided with this Diagram that are very useful in the understanding of how the visual system operates and also how man-made equipment interacts with the system. For the first time, it becomes possible to specifically define “color,” “white” and specific colors based on physical (as opposed to psychophysical) parameters.

The combined luminance/chrominance sections present a new Sensation Space that is rigorously definable and theoretically defendable. It is shown that the brightness (perceived luminous intensity) is not directly relatable to the perceived chromatic hue or saturation in perception space. It is also seen that the conversion of brightness into luminous intensity in stimulus space is not represented by a fixed function, but by a complex adaptation

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[2]Wright, D. as reproduced in Boynton, R. Op. Cit. pg. 397-403

[3]Judd

environment. As a result,

+it **is not possible** to define a meaningful three-dimensional luminance/chrominance space in an equidistant coordinate system in stimulus space.

+it **is possible** to define a meaningful three-dimensional brightness/chrominance space in an equidistant coordinate system in perceptual space.

Chapter 17 also shows that the variability in the gain of the individual spectral channels, colloquially known as adaptation, plays a major role in the brightness constancy, the color constancy, and the temporal constancy (or lack thereof in each of the above) of the visual system. The subjects of brightness and color constancy are quite closely related.

> In the case of brightness constancy, the gain of the adaptation amplifiers changes in unison in response to **spectrally uniform intensity changes** within the photopic region.
>
> In the case of color constancy, the amplifiers change independently in response to **spectrally non-uniform intensity changes** in input stimulus.

The underlying mathematical function is shown to be quite different from that normally assumed. The underlying functions are shown to be solutions of a second order differential equation with variable coefficients. They apply to all spectral channels individually, do not involve rods and cones as a functional concept, and can be described as "expanded sinusoidally modulated exponentials." This formulation is in complete agreement with the experimental data base–and provides the only explanation in the literature for the characteristic rise in the dark adaptation function after 25 minutes duration.

Chapter 17 treats the subject of spatial performance in less detail. This subject is considered to involve a separate effort and be out of scope for this work. There are several reasons for this. The spatial organization of the retina with respect to both Stage 1 and Stage 2 are still not understood. The fact that much of the signal processing related to spatial detail is actually performed in temporal signal space has not been considered in most of the prior experimental activity. Finally, the subject requires a greater understanding of the feature extraction engines of the cortex than is currently available.

Chapter 18, Clinical electro-physiology & visual Abnormalities in Man, cannot be addressed in depth in any single volume. The amount of anecdotal material and the lack of a theoretical model to provide consistency in the material makes its organization difficult. However, a framework is provided for future work that includes a new nomenclature for describing abnormal vision. This framework is used to quantify a wide variety of defects in vision as presented in the literature. It can also be used to interpret and organize the many transient spatial and temporal effects of vision. The Chapter also discusses briefly the difficulty of inferring a genetic cause for abnormal visual performance without an adequate model of the system. The visual system is too complex to assign a single point of failure to most cases of abnormal vision. With multiple points of failure associated with a single observed failure mode, it is difficult to assign a single genetic code failure to this mode.

Chapter 19, Mechanisms and Capabilities of Reading, has recently been added. So much new material was incorporated into Chapter 15 that it became possible to describe for the first time how humans actually read. The material is not limited to empirical data. It provides the first published detailed theoretical model of the reading process. With this model, it becomes possible to present simpler models that describe various phases of the reading process. It also becomes possible to delineate various failures typically found within the system. The discussion highlights the importance of learning and memory within the human visual system. It also shows that the striate cortex (the so-called primary visual cortex) of the occipital lobe of the neo-cortex plays a minor role in reading.

Chapter 20, Comparing Different Theories of Vision, attempts to categorize the alternative theories of vision based on their physiological origin and in some cases, their use of analogy. In the absence of a comprehensive model of the visual process in animals, there has been an immense proliferation of “floating models” addressing only a small area of vision. These floating models are generally unresponsive to the boundary conditions placed on them by the requirements of other elements of the vision process. Most of the alternative theories of vision depend upon “floating models.” Only a limited amount of space can be allocated to these theories in the final chapter.

The oldest overall theories are generally based on psychophysics (Young-Helmholtz and Hering) and can be seen to be subsets of the theory presented here with additional caveats limiting their range of applicability. Morphological theories related to vision generally start with Cajol at the end of the 19^{th} Century with a constant (and fruitless) struggle to define two distinct classes of photoreceptors continuing to this day. Morphology (and cytology up to the present) has proven to be the wrong tool to define the spectral classes of the photoreceptors and to define the functional characteristics of the neural system. The Chapter presents an alternative to the recent glutamate theory as it applies to the function of vision. The glutamate theory is seen to depend on an illusory cell membrane surrounding the Outer Segments of the visual process. Because of the difficulty of proving a negative, VISION CONCEPTS has offered a reward for anyone who can demonstrate the positive, the existence of a true cell membrane surrounding the disk stack of an Outer Segment in chordates.

Chapter 20 compares this first comprehensive theory of the functional, and end-to-end, operation of the neural system with the current “excitable axolemma” theory. The former is based on the active electrolytic semiconducting device, the Activa, involving the appropriate juxtaposition of two lemma in order to elicit “transistor action.” Transistor action is a well explored and understood fundamental mechanism of semiconductor physics whereas the excitable axolemma remains only an un-demonstrated concept. The comparison is one-sided since the excitable axolemma theory has never reached the point where it can predict the detailed performance of a circuit such as the photoreceptor cell, the Node of Ranvier as a signal regenerator, the retinal ganglion cells as encoders, or the detailed operation of any other neuron. The excitable axolemma theory does not offer any explanation for the ability of the neuron to produce an output signal that is inverted with respect to one input while not being inverted with respect to a second input to the same neuron.