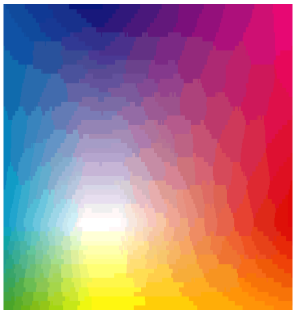

PROCESSES IN BIOLOGICAL VISION

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Synopsis [1]
(made available for comment)

Background

This work originated in the 1960's with the realization that rhodopsin, as then defined, did not meet the requirements for being a chromophore. It was particularly deficient in the structural characteristics required of a good chromophore. This was understandable in light of the limited tools available in analytical chemistry of that period. The basic assumption had been that the residues of a destructive process could be easily returned to their original state and that state was a simple chemical bond involving only two components in a single molecule. This could be done conceptually and hopefully in the laboratory. The problem was the characteristics of the residues were not actually known. It was assumed that one of the residues was the alcohol **or** aldehyde of Vitamin A. The other residue was assumed to be a protein and was given the name opsin. Valiant, but unsuccessful, efforts were made to define the nature of the molecule and achieve the formation of rhodopsin in the laboratory.

A new class of retinoids was defined by the author at that time, the Rhodonines. This class met the requirements of physical chemistry and photochemistry for a high performance chromophore. However, it was difficult to obtain acceptance of the Rhodonines as a replacement for Rhodopsin within the vision research community. It was obviously necessary to place the material in a larger context to obtain such acceptance.

It was clear from work reported in the 1960's that the Rhodonines were actually present in the liquid crystalline state when employed in the vision process. This state accounted for their remarkably high absorption coefficient as well as their unique spectral absorption characteristics. However, this state of matter was virtually unknown to the Vision Research community.

More recently, the author undertook to determine the functional description of the photoreceptor cell and its relation to the photoexcitation process. This process produced remarkable results. It led to the discovery of the active mechanism involved in signaling common to all neurons. The Activa is an active three terminal electrolytic semiconductor device. The Activa is the electrolytic analog of the solid state transistor. A basic utility Patent has been awarded by the US Patent & Trademark Office relating to this discovery.

To properly understand the functional operation of the neuron, it is necessary that the reader be familiar with the concept of a “hole.” In brief, a hole is an absence of an electron in a crystalline lattice. A hole can be described as a positive charge that moves in the opposite direction to an electron under electrostatic forces. The hole has only appeared recently in the literature of the bio-electrolytic chemistry field; a situation similar to that in solid state semiconductor theory in the 1950's.

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A major corollary associated with the discovery of the Activa was that the fundamental active mechanism within a neuron is an analog mechanism. It may not receive the appropriate emphasis but the vast majority of the neurons in any animal are associated with the sensing and inter-neuron processing of signals. These neurons all operate in an analog signal environment. It is only the signal projection neurons that employ pulse techniques to minimize energy requirements. They generate the "action potentials" so well known in neuroscience by the same simple process used widely in solid state transistors.

Following the discovery of the basic signaling mechanism of the neuron, its location within the neuron but external to the nucleus became obvious. The general location was already described in the literature. Several discoveries occurred following the discovery of the basic signaling mechanism. The most important was the discovery that there were two primary applications of the Activa in vision, and in fact in all neural systems. The Activa represented the signal manipulation device at the dendrite-axon interface inside a given neuron. The Activa also represented the primary signal transmission device at the axon-dendrite interface between neurons, the so-called synapse. These two discoveries place the signaling function of the neural system in animals on a firm electronic foundation.

Scientific Perspective

The work opens with a major **Part A** devoted to the physical environment and the phylogenic tree of the animal kingdom. It is necessary to explore many of the ramifications of how animals exist in their environment in order to provide a framework for a global analysis of the visual process. An initial finding was that the common division of animals into two major branches, protostomic and deuterostomic, is not an appropriate one. It became clear that vision has evolved along three different paths in conjunction with the three large animal classes; *Arthropoda, Mollusca and Chordata*, more colloquially described as the insects, the molluscs and the vertebrates. The amount of differentiation within each class has caused significant areas of overlap in the visual processes of these classes. However, the class relationship must be respected if a true understanding of the visual process in a given species is to be obtained.

This part also demonstrates that first order or so-called Gaussian optics can not be relied upon in vision research. Gaussian optics are limited to the paraxial condition, i.e., less than one degree from the optical axis. The fovea is slightly more than five degrees from the optical axis. This fact and the high curvature of the retina calls for the use of a full optical analysis, including fifth order aberrations, in visual research.

Part B focuses on the photochemistry of the visual process in detail. **Part C** follows as an unanticipated drop-in part. It concentrates on the newly discovered functional mechanism within the neurons of all animals with particular focus on the visual system. To appreciate this Part, it was necessary to expand and codify the terminology of the neuro-scientific literature. **Part D** takes the knowledge developed in the earlier parts to develop the signaling environment of the visual system and closes with an interpretation of the resulting psychophysiology applicable to all animals but with a special emphasis on human because of the breadth of the literature available in this area. **Part E** presents both global and specific analyses describing the visual system in animals. This analyses also includes Sections on failures in the system as well as abnormal or aberrant operation of the visual system. It closes with a discussion of areas of further study and a preliminary summary of productive experiments.

The work concludes with a comprehensive **Glossary** and a large number of **subject specific appendices** in support of the main work. These appendices go into much greater depth in specific areas. They include tabular descriptions of **A Standard Eye for Research in Human Vision** and **The Functional Aspects of the Neuron.** They also include **a detailed electrolytic circuit diagram of the human retina**. There is also a detailed comparison of solid state and electrolytic semiconductor devices, transistors and Activas.

The Photodetection Process

With the above foundation, it became possible to understand the operation of the photodetection process. This explained the operation of the Outer Segment associated with the photoreceptor cell as well as the operation of the photoreceptor cell itself. The results were very satisfying. The results led directly to the Photoexcitation/De-excitation equation that described the generator waveforms found at the terminals of the photoreceptor cell/Outer Segment association. The word association is used because it became clear that the Outer Segment is not an integral part of the photoreceptor cell. It is a structure extruded by the photoreceptor cell and, therefore, found outside the cell membrane.

With the modern tools of physical chemistry and electrical engineering available, it was possible to define the structure of the Outer Segment in considerable detail. This led to the determination that the spectral absorption characteristics of the chromophores, when deposited as a liquid crystal, on to a substrate in more detail. This solved one of the classic problems of experimental electrophysiology as it applies to vision. The Outer Segments exhibit a distinctly anisotropic absorption spectrum. The distinction involves two separate mechanisms. Each of the chromophores in the Rhodonine family exhibit a common isotropic absorption spectrum with a peak absorption wavelength near 500 nm. This spectrum is due to the monopolar characteristics of the molecules conjugated hydrocarbon backbone. Simultaneously, when in the configuration found in the Outer Segment, i.e., a liquid crystalline state of flat surfaces, the molecule exhibits a second highly directional absorption spectra particular to its unique bipolar physical chemistry and conjugated hydrocarbon backbone. This absorption spectra has a strong peak at its characteristic chromophore wavelength to light applied axially to the Outer Segment. Thus the dichotomy between the results of reflective spectrophotometry through the iris of the eye and the results of transverse spectrophotometry performed in a variety of electrophysiological experiments.

With an understanding of the quantum mechanical operation of the chromophores applied to the substrate of the disks, it became possible to explore the interface between the Outer Segment and the photoreceptors in more detail. The ramifications of this exploration were significant. They included:

> the confirmation of the unique two-exciton process found in the long wavelength photoreceptor channel of animal vision and predicted from the laboratory results in man regarding the photopic and scotopic spectrums as a function of illumination level.
>
> the demonstration of the fact that there are no achromatic photoreceptors in animal vision.
>
> the recognition of the extremely high effective quantum efficiency of the visual process in animals--rivaling successfully the highest quantum efficiency achieved in man-made semiconductor based sensors (>90-95%) and far higher than that achieved with photoelectric tubes (including the photo-multiplier types).
>
> the location of the adaptation amplifier that; controls the signal level in the remainder of the visual signal processing chain and accounts for the remarkable dynamic illumination range of the animal eye. [The term dynamic is used to indicate that the instantaneous range is limited to only about 120:1 within a total range exceeding 1,000,000:1.]
>
> the corroboration and explanation for the ability of the animal eye to detect individual photons. This corroboration also defined explicitly the fact that the chromophores of vision are not energy detectors--they are quantum detectors. The use of equal energy spectral signals in vision research is not appropriate and leads to fundamental errors in calibration and measurement if not accounted for.
>
> the recognition of the second class of Activa within the photoreceptor cell which acts as a distribution amplifier serving the synapses associated with the pedicle.

The Signal Processing within the Retina

With the nature of the signals available at the pedicle of the individual photoreceptor cells understood, it was possible to categorize the photodetection channels of vision and to explore the signal processing functions of the retina more precisely. This has led to a clear distinction between the three broad classes of signal processing within the retinas of all animals, with emphasis varying between species, the luminance, chrominance and appearance channels. It is not possible to explore the appearance channel of animal vision extensively at this time because of the limited scope of the literature. However, it was possible to explore the luminance and chrominance channels in considerable detail. This effort uncovered four extremely important features of all animal vision:

> the fundamentally tetrachromatic aspect of animal vision, the ultraviolet capability being lost in atmospheric animals employing complex eyes due to the absorption characteristics of the cornea-lens combination.
>
> the generation of both the exact photopic and exact scotopic spectral response (as well as the intermediate mesopic and the hyperopic spectral responses) of the complex eye based on the input of signals from only the chromatic signal channels associated with photodetection. There was no need for a so-called rod sensor, an achromatic sensory channel.
>
> the fact that the typical animal eye incorporates three chrominance difference channels, only two of them being active in atmospheric animals with complex eyes--such as humans.
>
> the fact that the signal projection elements of the visual system were fundamentally transparent to the signals being carried. This resulted in a quasi-perceptual plane located at the input to the ganglion cells that closely mimicked the putative perceptual plane within the brain. The failures in the signal projection elements to be transparent are the source of most of the erroneous perception related flicker phenomena observed in human vision.

With a quasi-perceptual plane recognized within the retina, it becomes possible to explore the signal projection elements of the visual system in more detail. This exploration quickly defined the nominal role of the ganglion cells, the mode of signal encoding used and certain secondary characteristics of interest.

The ganglion cells are seen to be simple reflex oscillators of a well known type. They can operate in the mono-pulse, bistable or astable mode depending on the function required, and occasionally on how they are treated (abused) by an electrophysiological experimenter. The ganglion cells associated with the chrominance channels, believed to be the midget ganglion cells, normally operate in the astable (or free running) mode. The ganglion cells associated with the chrominance channels normally oscillate at a pulse to pulse interval of about 33 milliseconds, near the fusion frequency of the human eye.

The ganglion cells associated with the luminance channel, believed to be the parasol type ganglion cells, operate in a somewhat more complex mode. In the absence of photoexcitation, they operate in the astable mode. Upon photoexcitation at a level exceeding the ganglion cell threshold, they generate a single pulse, known as an “action potential.” If the photoexcitation remains above the threshold or increases, the ganglion cell generates additional pulses with a time interval between pulses indicative of the strength of the signal.

The signal in the luminance channel is seen to be encoded using time delay between pulses as the “carrier.” This signal encoding mode is known as time delay modulation, a common form of phase modulation. It is important to note that the modulation is not frequency modulation. Frequency modulation cannot carry information in as compact a form as phase modulation. Normally frequency modulation cannot carry any information concerning the first pulse. The initial pulse in the luminance channel is used in conjunction with the tremor to indicate alarm or change. The same type of encoding is used in the chrominance channels except for an offset. The time duration before or after the occurrence of the nominal pulse is used to encode a bimodal signal. When encoding high saturation color information, the resulting signal is asymmetrical. This asymmetry is the source of most distortions associated with flicker phenomena.

It is very easy to implement a signal decoding circuit in the brain using a single Activa per projection path. Subsequent signal processing in the immediate vicinity of the decoding Activa is analog in nature. Only when information must be transmitted over distances longer than a millimeter can one be assured that an additional encoding step will be involved using a projection neuron similar to a ganglion cell.

Theoretical Results

There are several major theoretical results that can be categorized with respect to:

> the fundamental active device underlying the mechanism of the neuron,
>
> the underlying architecture of vision,
>
> the underlying equations of vision, and
>
> a set of graphical descriptors illustrating the capabilities of the visual system.

There are several major theoretical results:

> the demonstration of the critical role played by the liquid-crystalline state of matter, and the unique electrolytic properties associated thereto, in the vision and neural systems
>
> the demonstration of a new photochemistry for the photodetection process in all animal vision
>
> the discovery of the Activa as the primary mechanism of the neural system in all animals
>
> the discovery and demonstration of the fact that the visual and neural systems do not employ dissipative thermodynamic principles.
>
> the demonstration of the fact that feedback, in its external form, is not used in the visual process
>
> the recognition that feedback, in its internal form, is key to the operation of the photoreceptor cells

The discovery that the entire neural system operates under reversible thermodynamic principles in order to achieve its unique level of thermal efficiency is fundamental. This discovery also places the subject of bio-energetic fuels to support the neural system in an entirely different light. It provides conclusive evidence that the fuels represented by the glutamates, GABA and the non-protein amino acids, such as glycine, do not participate in the signal detection, processing or transmission process in vision but are critical to the power supply function associated with the electronic nature of the neural system. In this role, the density and consumption of the bio-energetics associated with a photoreceptor cell is proportional to the illumination level. The density and consumption associated with other visual cells is less direct. These bio-energetics are required by every neuron. They are known to be ubiquitous throughout the body.

> **All of the above and following postulates are overwhelmingly supported by the available literature and the experimental work of many individual investigators.**

Practical Results

Based on the above finding, described in detail and documented in this work, it is possible to develop several important practical results and applications. The overriding result of this work is a contiguous theoretical model applicable to the *Visual Process in All Animals* with its associated equations and demonstrations of applicability.

Fundamental

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The most important practical result is the elimination of the putative achromatic "rod" from further research interest. All animal photoreceptors employ one of four chromophores, three in atmospheric complex eyes, from which all achromatic and chromatic information is extracted. The second most important result is the recognition that vision does not involve linear signal processing. The common linearity laws do not apply. In fact, a majority of the visual signal path employs "large signals" at all times. This makes even the imposition of linearity based on the small signal model inappropriate at light levels above that equivalent to the full moon. Analysis of the visual system at the research level requires the use of logarithmic algebra. The third fundamental result is that external feedback is not employed nor is any form of retro-signaling, such as dendrite to axon or dendrite to dendrite.

Photometry

Although it may continue to be useful for engineering purposes to use empirical values for the spectral performance of the animal eye, ***a single equation is now available that defines the radiometric performance of the eye under all slowly changing irradiation conditions***. These conditions range from the hyperopic thru the photopic and mesopic to the scotopic. A perturbation analysis of this equation at a given irradiance provides clear indications of the rigor required in laboratory investigations if useful data is to be obtained. A simple calculation also becomes available to indicated the error inherent in using a fixed spectrum photometer, particularly one employing an energy sensitive detector, to simulate actual visual performance.

Colorimetry

With the actual equation available describing the spectral absorption performance of the eye, it is no longer adequate to assume the *trichromatic generalization* is true. This generalization is based on a group of linearity laws that are not applicable to the vision process when studied from the research perspective. Specifically, what is known as The Color Equation, the linear sum of the contribution of each chromophoric channel represents the total chromatic experience, is now archaic. At the research level, logarithmic algebra is required.

Imposition of logarithmic algebra has many benefits. It negates the need for such empirical tools as "tristimulus values, including putative real and imaginary spectrums. The word real in the previous sentence refers to "realizable but synthetic spectrums", not to actual spectrums. The use of logarithmic algebra also obsoletes the C.I.E. Chromaticity Diagram for research purposes. ***A New Chromaticity Diagram*** *suitable for research purposes is now available* which involves orthogonal coordinates in either two or three dimensions. Only the two dimensional version is needed for humans and other complex eyes within the atmosphere.

The New Chromaticity Diagram solves the century old battle between the Hering and Helmholtz schools. It provides the theoretical foundation upon which to evaluate the proposals of both schools and the associated shortcomings of each theory.

The theory defines and The New Chromaticity Diagram illustrates that the sensation of "White" is uniquely defined in perceptual space. The white of perceptual space is transformed uniquely into object space when the object space luminance represents an equal photon flux spectrum. If the large field object space luminance is not represented by an equal photon flux spectrum, the adaptation amplifiers in each photodetection channel will attempt to compensate for this fact. This compensation manifests itself in two ways:

> No matter what the large field object space luminance is, the eye will still perceive the sensation of white in the perceptual plane. Knowing the state of the adaptation amplifiers, one can transform this perception back into object space.
>
> The unitary white point in perceptual space is transformed back into a series of white points in object space for different photon flux spectrums. The C.I.E. has defined a variety of specific photon flux spectrums using the term luminants, i.e., luminants A, B, C and more recently D_{65}, etc.

Thus, the Theory, model and equations clearly demonstrate that the linear addition of pigments and lights in object space must be clearly differentiated from the chromatic response of the organism in perceptual space. These two representations of color are only related by a very complex mathematical transform at the research level. The transform can be simplified for engineering applications as long as the appropriate caveats are noted.

The theory and equations also define explicitly how the sensation of color is lost as the luminance level is reduced, leading to achromatic perception at scotopic illumination levels. As long as the adaptation amplifiers are operating at less than maximum gain, they produce an essentially saturated chromatic signals at the input to the chromatic differencing circuits. The result is a variation in perceived hue that can be accompanied by high saturation levels. At lower illumination levels, signals at the input to the chromatic differencing circuits are reduced in amplitude. The resulting difference signals are also reduced in amplitude. As a result the signals applied to the midget ganglion cells are reduced and the level of modulation of the encoded information is less. When detected within the brain, only reduced levels of saturation can be perceived, eventually leading to a perception that is limited to white and black. This occurs at scotopic levels. No achromatic photodetectors, “rods,” are required in this process.

Geometry

The signal processing related to the geometry of scenes has not been treated in as much detail as the photometry and colorimetry of the visual process. This is due to a paucity of detailed information to draw on. This paucity is in turn due to the complex relationship between the spatial and the temporal performance of the visual system. The block diagrams and schematics applicable to the appearance signal processing channels have been outlined. These outlines should encourage further experimental activity.

Circuits

Individual circuit diagrams are presented for each stage of the visual process, photodetection, or signal detection; luminance, chrominance and appearance signal processing; and signal transmission or projection. These actual biological circuit diagrams can be emulated using electrolytic (either biological or non-biological) semiconductor or solid state semiconductor devices. These circuits were emulated in the solid state for the military during the 1970's. The purpose was to demonstrate feasibility of a 100,000,000 detector mosaic for Inter-continental Ballistic Missile (ICBM) tracking.

Transient & other second order effects

With a detailed model of the visual system of any animal available, it is possible to explain in detail most of the many transient and unusual effects recorded in the literature under the names of various investigators. These proper name references can now be dropped in favor of more specific mechanism related names.

Pathology and Medicine

The overall model and the equations provide a new and unique ability to aid the clinician in the isolation of medical problems. The model also provides for the first time a definitive description of the types, sources and potential medical cures for a wide gamut of color vision abnormalities. The model and equations are able to help immensely in the attack on the more intractable problems of current visual pathology.

Summary

This work has provided a new and much broader understanding of the Process of Animal Vision. However, to appreciate the visual process, certain revisions in the conventional wisdom must be made. These revisions involve our understanding of certain fundamental physical and mathematical concepts, certain realizations about the basic processes of vision, and many of the tools used in visual research. These revisions have led to a variety of important discoveries.

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Foundations

To understand the operation of the animal visual system, it is mandatory that some broadening of the accepted concepts be employed:

+It must be recognized that there is a fourth state of matter, the liquid crystalline state, that is present ubiquitously in living organisms and exhibits many unique properties in the operation of the organism.

+ It must be recognized that Gaussian statistics are not appropriate to many visual processes and events. Gaussian statistics are an approximation, for large aggregate quantities, to the more fundamental Poisson statistics. Poisson statistics hold for small quantities as well as large in the absence of other "control parameters." Statistical events involving quantum events include an additional control parameter, Pauli's Exclusion Principle. These events, such as photodetection, are represented by Fermi-Dirac statistics. Statistical events involving biological growth also involve a (different) control parameter and are represented by Poisson statistics in logarithmic quantity space. The resulting statistics are frequently approximated by log-normal statistics (or log-Gaussian statistics). The data can be approximated by a "bell shaped curve" on a logarithmic horizontal axis.

+ It must be recognized that the thermodynamics taught in general education, and involving a Carnot Cycle, is not the only form of thermodynamics. The Carnot Cycle is based on the assumption that some heat is generated in the process under discussion. Many reversible electro-chemical reactions do not release heat. These reactions operate in accordance with the laws of reversible thermodynamics. The electrostenolytic processes employed in the neurological system involve reversible thermodynamics.

+ It must be recognized that the presence of a material ubiquitously in the neurological system does not mean it is a participant in the signaling function of neurons. In the neurological case, there are two environments in the vicinity of the neuron interconnections (synapses and Nodes of Ranvier). In the perinodal area, the dominant material is a minute liquid crystal of pure water (hydronium) and the signal carrying charges are electrons and holes. In the paranodal area, the most important materials with respect to vision are the bio-energetics participating in an electrostenolytic process and related to the glutamates and butyrates (simple amino acid derivatives). The charge carriers in the electrostenolytic processes are electrons and ions. The transport of ionic materia within the paranodal region does not constitute signal transmission.

+ It must be recognized that vision, and the operation of the neural system in general, is a non-linear process involving logarithmic mathematics.

+ It must be recognized that many families of Retinoids, and the properties of the liquid crystals, were unknown at the time that the basic assumption was promulgated that the photoreceptors of vision involved Vitamin A in simple molecular union with a protein. Definition of the Rhodonine family of Retinoids provides the actual chromophores of all vision when present in the liquid crystalline state and in electronic contact with the neurological system (or other discharging mechanism.

Based on the above facts, it is possible to summarize the fundamental findings of this work.

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 process.

Superposition, based primarily on Linearity, is not applicable to the visual process, even under small signal conditions when investigating color perception.

The photodetection process involves a mixture of linear and square law processes.

The high degree of negative internal feedback within the photoreceptor cells allows the entire remainder of the visual system to operate in a mode defined by a fixed amplitude range, which must be considered highly non-linear.

Tools

It must be recognized that the tools developed in the 1930-60 time frame by the C.I.E. do not rest on the foundation and realizations outlined above. Whereas these tabulations and diagrams are adequate for normal engineering applications, they are not adequate for research purposes.

Based on this work, the various empirically based and discrete luminosity functions, photopic and scotopic, can be replaced by a theoretically based and continuous luminosity function that can be considered to include four discrete regions; hyperopic, photopic, mesopic and scotopic.

Based on this work, the empirical C.I.E. Chromaticity Diagrams can be replaced by a theoretical New Chromaticity Diagram for Research. This New Chromaticity Diagram is free of the many ambiguities and imprecise aspects of the old diagrams.

Based on this work, the old empirical “dark adaptation curve” can be replaced by a new theoretically based “full adaptation function” that incorporates both the old “dark adaptation curve” and the virtually non-existent “light adaptation curve” as special cases. The resulting function dispenses with the notion of “rods” and “cones” and correctly describes the transient response of the eye under a variety of conditions involving illumination intensity and spatial position. The function clearly presents the state variable nature of the visual process.

Discoveries

1. The discovery of the actual chemicals (the Rhodonines) involved in 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 to 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.* The mechanisms do not employ a Carnot Cycle, 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. It is the simplest and easiest to study of all synapses. Functional synapses, by one name or another occur between neurons as well as within cell bodies.

The book contains 19 generously illustrated chapters, includes a six-page summary of the tabular parameters of the human eye, an extensive glossary and approximately 10 appendices. A more complete description of the book, a summary of the hypotheses within the Theory, and sample chapters are available at the Vision Concepts website.

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