PROCESSES IN BIOLOGICAL VISION:

including,

ELECTROCHEMISTRY OF THE NEURON

This material is excerpted from the full β-version of the text. The final printed version will be more concise due to further editing and economical constraints. A Table of Contents and an index are located at the end of this paper.
15 Higher Level Perception–
PART I
Signal (Vector) Interpretation

This chapter has been divided into two PARTS because of its size and the rapid advances being made in the understanding of the operation of the brain. This PART I is concerned with our understanding of the operation of the brain, as reflected in the journal literature, up to the middle of the 1980's. PART I still includes considerable material not available in any other text published through the 1990's. PART I contains a description of the cortical portion of visual system and human brain current as of the 1998 time period and the processing of visuotopic (as opposed to abstract) signals. This description is sufficiently advanced, relative to the literature that it forms an important bridge leading to the more advanced material in PART II. PART II introduces the important results of the Brain Research community as they apply to an understanding of the complete visual system. It contains a further expansion on the figures found in Part I in order to describe our knowledge of the system circa 2002. The major new material deals with the critically important role of the thalamic reticular nucleus of the diencephalon portion of the “old brain.” Its focus is on the extraction of abstract signals from the visuotopic signals presented to the feature extraction engines, and the ultimate processing of those signals.

15.1 Introduction UPDATE re 15.6

Our understanding of the functional elements of the diencephalon and mesencephalon is maturing rapidly. This makes it difficult to keep this chapter current. A particular problem concerns the engines found in the space morphologically labeled the thalamus and superior colliculus. In some cases, the literature cited will use the term pretectum of the tectum for what is becoming known as the perigeniculate nucleus of the thalamus. Part II of this chapter will provide further details in this area.

This Chapter will discuss higher level (both sub-cortical or old brain and neo-cortical) signal processing occurring in the CNS. This processing will be called signal manipulation for clarity. Of more importance, it will discuss the “context” in which imagery is manipulated and stored. The subject of morphology will not be addressed in detail but the anatomy and topology of the nervous system will be. As discussed in the introduction to PART D, stage 4 of the visual system includes both perceptual and cognitive functions. The literature of cognition is very large. However, prior to the development of MRI, PET and CAT imaging techniques, it has been a very immature field. Although interesting concepts have been put forward for discussion, cognition remains poorly understood. At the perceptual level, more progress has been made, helped immensely recently by the development of the above imaging techniques.

Spillmann & Werner have published an excellent compendium of the state of knowledge regarding the operation of the cerebral cortex, circa 1990, based primarily on psychophysics, clinical experience, anatomy of the cortex and some cytology. Some differences in terminology and notation will be used in this work for reasons explained below. Much less is known about the function and capability of the cerebellum. Based on this work, its role appears to be of paramount importance in the efferent signal paths of vision.

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1Released: August 30, 2013
More recently, an event of major importance has occurred. Semir Zeki of University College London, a prolific writer and leader in the investigation of the visual system of the brain, experienced an epiphany. His book of 1993 reflects his paradigm shift in thinking as do his articles subsequent to that date (see the preface, prolog and epilog). He apologizes for his long allegiance to the conventional wisdom of the last century and explains how his work subsequent to the early 1980's has forced this major change. The seeds of the change are seen in the series of papers he presented in block in 1978 where he notes the absence of an intersection between the vertical and horizontal meridians in V1 and the presence of signals in V4 that cannot be traced to V1. His epilogue in that book should not be overlooked. His new paradigm still suffers from the lack of a viable model of the visual system adequate for his purposes. Lacking such a model, he still supports the conventional concept of morphologists that “form dictates function.” However, his support is greatly diluted and continuing to fade (see his 1995 paper with Becker). His concept of the cause of the putative phenomena of color constancy is still inadequate. Lacking a model, he also continues to speak of the M and P pathways in a nebulous manner, exhibiting little appreciation of the multiple classes of signals being carried by these pathways.

Zeki’s new concept of the brain is as a modular system without a hierarchal structure and with multiple input pathways from the sub-cortical areas. This work is in total agreement with his new concept. However, his lack of a model constrains his interpretation at the detailed level. A better model would also provide a clearer understanding of the transform between motion in object space and the waveform parameters in temporal space that must be converted back to a vector representative of said object space motion. In the following material, the data of Zeki is used extensively in support of this work. Opposition will be taken to many of his positions in his pre-1990 articles. However, it appears he no longer supports these older positions (See Ffytche, Guy & Zeki and Beckers & Zeki below).

Most of the textbooks of the 1990's and 2000 have not incorporated Zeki’s new views. This is unfortunate. His views are being confirmed daily using the newer techniques of nuclear imaging and his additional technique of magnetic interference. Tootell & Hadjikhani have recently provided additional data on this question of the existence of a V4.

In the magnetic interference technique, Zeki is using very high strength magnetic fields to disturb the electrical conductance of signals within the brain. This technique shares with his earlier degenerative techniques, involving lesions, an inadequate spatial specificity and no known direct relationship with the underlying mechanisms. It is also difficult to implement because of the folding of the cortex.

Crick & Koch provided a provocative article entitled Consciousness and Neuroscience in 1998. It followed a paper that generated mild turmoil in the neuroscience community by stating the obvious. They took the position that a subject “is not directly conscious of the features represented by the neural activity in primary visual cortex” (V1). The “extremely schematic diagram” of Figure 1 in the 1995 paper is obviously inadequate for their purposes. The 1998 paper includes a mini-review as well as a series of hypotheses. Their premises appear to be based on good logic, using a variety of anecdotal experimental results, but lack a sufficiently detailed model to avoid argument. Their task is complicated by the lack of sufficiently specific definitions of the terms used. While the discussion between Crick & Koch, and others like Pollen, are applauded, their lack of precision prevents this author from

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More specifically, the hypotheses of Crick & Koch do not recognize the multiple signal paths through the brain related to visual signals. They rely upon a simple ladder concept attributed to Fuster. One leg of the ladder relates to afferent pathways and the other to efferent pathways. The approach is similar to that discussed in Section 11.1.4. The brain is much too complex to continue to be represented by such a simple framework. A more elaborate ladder will be presented in Section 15.2.2. This ladder, along with the top level schematic diagram of chordate vision in Section 15.2.3 provide a framework sufficient to discuss many of the terms used in the above articles. They also help provide a clearer separation between terms like perception and recognition. The concept of a zombie becomes much clearer using these models. As Crick & Hoch describe the zombie conceived by philosophers in their carefree way, a zombie “is supposed to act just as normal people do but to be completely un
conscious.” By using the models of this chapter, additional differentiation can be introduced into what a zombie can and cannot do.

The Crick & Koch paper was focused on locating the “neuronal correlate of consciousness.” Their initial thoughts are provided in a section called “clearing the ground.” There, they scope the difficulty of the problem and why many feel it is premature to search. Like so many others in their field, they disparage the “premature definition” when discussing the word conscious. However, they seem to be comfortable with working definitions, particularly in the area of visual consciousness. Their unsupported claim that the visual system of other primates is similar to that of humans is not supported by their notice of the “present miserable state of human neuroanatomy.” It is not accepted here. At the level of perception and cognition, the human system is distinctly different from that of all other chordates. One of the most capable of the family Pongidae, the chimpanzee, Pan troglodytes, still appears inadequate compared to Homo Sapien in these areas (Section 1.2.1.5.5).

Crick & Koch stress the necessity of a saliency map without using the term. They state “to be aware of an object or event, the brain has to construct a multilevel, explicit, symbolic interpretation fo part of the visual scene. By multilevel, we mean, in psychological terms, different levels such as those that correspond, for example, to lines or eyes or faces. In neurological terms, we mean, loosely, the different levels in the visual hierarchy.” It is not clear their two uses of the term multilevel are consistent. As will be shown in Section15.2.2, the term aware best used with an adjective to differentiate between perceptual awareness and cognitive awareness. It is also important to note the difference between tonic and phasic neurons in the CNS. As noted in Chapter 11, only a few percent of the neurons of the brain create action potentials (by firing). Most of the signal processing within the brain is accomplished within the tonic domain. The signals are only converted to phasic form for purposes of transmission between engines. The fact that most memory and signal processing functions are accomplished in the tonic domain change the tone of many discussions related to cognition. Their focus on a set of neurons firing as an ensemble to indicate cognitive awareness of a “face” appears to be associated with the ganglion cells at the output of a particular engine. In this case, they are in fact expressing the phasic condition associated with the tonic equivalent condition within the engine.

Using the top level schematics of Section 15.2 and 15.6, the premise of Crick & Koch is found to not differentiate between the awareness and analytical mode of vision. Further, they do not develop the close relationship between areas V1, V2, V3, etc of the occipital lobe. Recognizing that these areas operate in unison, their premise can be restated as: The perceptual awareness achieved by the LGN/occipital couple is not directly associated with the cognitive awareness associated with the higher cognitive centers of the cerebral cortex. Before cognitive awareness can be achieved, the information from the couple must be merged with other information and deposited (in abstract, or symbolic, form ) in the saliency map. This merging of information includes merging with information from the analytical mode of vision. Their notice of the fact that no direct signal paths have been found between V1 and the frontal lobe in macaques applies equally well to signal paths between the occipital lobe and the frontal lobe.

The complexity of the cerebral cortex remains beyond comprehension (even at the million-neuron-engine level) and the task of attempting to understand its operation is daunting. Progress has been made in a number of areas. However, the researcher must guard against oversimplification in his exposition. Humans like to simplify their
presentation and they love to focus on dichotomies. However, reducing the discussion of any significant phase of
the operation, topology or morphology of the brain to a dichotomy amounts to reduction absurdum. The larger
context must always be maintained. Van Essen has noted that the study of the cortex can be based on topographic
organization, anatomical connections, neuronal response properties, architectonics, and behavioural deficits resulting
from ablation. It has also been studied based on the projection of the topography of the retinas. This latter approach
is shown below to have limited applicability. It is suggested that a useful approach is to start with architectonics of
the brain, based primarily on exploratory anatomy associated with various sources of ablation, and correlating the
results with the signaling architecture of the retina and other pre-cortical links in the visual system. Using a tectonic
approach has been very useful to date and it continues to provide a firm foundation.

Baars & Gage published a textbook on Cognition, Brain & Consciousness in 20079. It is largely an introductory text
relying more on pictures than detailed discussion and not providing citations to many of the assertions put forward.

Baars & Gage made an astounding statement on page 60, “The great diversity of the neurons in the brain is
suggested by Figure 3.4–there are many classes of neurons, neurochemicals, and potential mechanisms of
information processing. Our first simplification, therefore, is to focus only on an integrate and fire neurons
(see figure 3.3).” The statement is astounding because it eliminates the granular cells of the brain from
their considerations. It is conservatively estimated (Section 10.1.2 & 10.1.3) that the granular cells
constitute more than 90% of the brain cells in the central nervous system. They have eliminated these from
their presentation!!! The number of granular cells increases periodically as more investigations using
electron-microscopy count granular cells not resolvable using visual microscopes.

Baars & Gage provided a 2nd Edition of their book in 2010 that moved their statement to page 65. The2nd Edition
includes a totally rewritten chapters 8, a major revision to chapter 12 and a new chapter 16 (related to the inferred
effect of genes on the neural system based on relatively old interpretations). The preface describes these updates in
more detail as necessary because the field is advancing like a “Big Wave” at Waikiki Beach. The book has an added
Pull Out section at the front and an extensive Glossary at the rear which are both welcome and important additions.
For the first time in a text, the resolution level of MRI techniques have allowed the LGN and the pulvinar to be
identified and their relevance discussed (in the rewritten Chapter 8).

The new chapter stresses the two-way communications intrinsic to virtually all thalmo-cortical and trans-cortical
commissure via the corpus callosum in line with the assertions of this work. The new Figure 8.10A and B are
interesting with regard to the dorsal visual path. Frame A shows the thalmo-cortical paths identified by MRI but
frame B relies upon a cartoon to identify the cortico-cortical paths (even though an associated inset does not justify
the cartoon). They then note (page 250), “Keep in mind also that the thalamus is the major input hub for the cortex,
and also the major cortex-to-cortex traffic hub. . .However, the basal ganglia operate as a major output hub, for
motor control and executive functions.” The subject of two-way communications is also addressed on page 252
relative to vision with “In fact, about 90% of the LGN-V1 fibers are ‘running the wrong way’. Above the LGN,
everything is a two-way highway. This is a dominant feature of the brain, and it is a great challenge to
understand how two-way connections work.” The emphasis was added because of the critical importance of this
statement. It is in agreement with the hypothesis of this work.

Until the arrival of PET, CAT, and MRI techniques on the scene, nearly all investigations of the performance of the
(recognized) visual portion of the brain involved electrophysiological probing. This probing invariably centered on
action potentials related to the projection neurons associated with the various regions of the brain. Negligible effort

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9Baars, B. & Gage, N. eds. (2007) Cognition, Brain, and Consciousness: Introduction to Cognitive Neuroscie...
was spent recording the actual analog signal waveforms related to the signal processing within a specific region. The newer non-invasive techniques have presented a different aspect of brain activity. It is based on the change in consumption of various metabolites in response to a stimulus. These techniques necessarily average the activity over an area of the brain delimited at least partly by the diffusion constants of those metabolites. At this time, both measurement techniques provide locations with large uncertainties with regard to precise location of a specific neural input or response. The recent data of Zeki and Marini is very useful in understanding the impact of specialized MRI on this field\textsuperscript{10}. However, the large areas recorded by Zeki and Marini cannot be considered exclusive to their specific stimuli. As shown in Robinson, et. al\textsuperscript{11}., the response areas of even simple stimuli exhibit a large area of overlap because of the complexity of the stimuli normally employed in the laboratory and the amount of signal manipulation employed. Such large degrees of overlap make it extremely difficult to assign a specific role to a specific morphological area. In the case of Robinson, et. al., their stimulus was a 3° by 3° white square, a stimulus considerably larger than the foveola, and therefore, representing a “mixed stimulus” in terms of the signal processing and perceptual systems.

It is necessary to point out that this work does not support the discussion in Zeki & Marini that rests on a computational foundation for the color constancy effect attributed to E. Land. This work has shown in detail that the observed color constancy effect is a function of the state of adaptation of the adaptation amplifiers within the individual photoreceptor cells. It is also shown that the signals presented to the LGN, PGN\textsuperscript{12} and ultimately the cerebral cortex are already “color constant” within the capability of the adaptation process. An auxiliary assumption in that paper, that the first wavelength-differencing operations occur in the cortex, is not supported by this work. There is a very large database in the literature, going back to the 1960's, showing that first wavelength-differencing occurs in the retina. The details of the mechanisms involved in achieving color constancy and color differencing are documented in detail in previous chapters of this work. The corroboration of these analyses is provided in the overall performance descriptors of the visual system developed in Chapter 17. The alternate hypothesis presented here may aid in the interpretation of some of Zeki & Marini’s results.

It has been traditional to work with test stimuli that are convenient in the laboratory rather than those related to the most important operational functions of the brain of the animal. From a functional perspective, the brain is assigned at least two major roles. The first, and foremost, is to support the organism in avoiding threats to its existence. This involves two primary roles, the earliest possible detection of threats followed by the earliest possible perception and evaluation of those threats. This second step need not be as complete as we humans tend to ascribe to it. The perception that a thrown spear will miss contacting us completes the threat evaluation process. Any subsequent evaluation to determine the characteristics or source of the spear are ancillary, even though they might help avoid a future threat and are useful. The difference between threat detection and threat perception suggest a division of the cerebral cortex that can be recognized in practice. Threat detection requires a set of sensory organs correlated as to “field of view” relative to an inertial platform and a knowledge of where every part of the animals body is located relative to that same inertial platform. The field of view includes not only the visual sensors but also the auditory and possibly other somatosensors (heat and touch for example). Notice how the auditory and somatosensory regions of the cerebral cortex, along with the higher areas of the visual system are all grouped in one area directly above the region of the super colliculus. This location tends to minimize the transport time of signals between the threat

\textsuperscript{12}The term pretectum is used to describe a group of nuclei of the thalamus, not including the LGN, concerned with the pointing of the eyes and the analysis of fine detail. See Glossary. Leventhal (1991) gives a thorough discussion of these nuclei. Carpenter & Sutin (1983) give a similar discussion, but with limited focus on vision. The more precise term perigeniculate nucleus (PGN) will generally be used as a synonym in this work.
evaluation and the kinetic response regions of the brain.

Another important conclusion of recent years is that the various regions of the cerebral cortex operate as modular units requiring variable amounts of signal manipulation. It has also been found in this work that the signals transmitted to the cortex vary considerably in arrival time due to the asymmetries of the signal projection circuit of stage 3 and the variable delays associated with the photoreceptor channels of stage 1. As a result, any high level perception and all high level cognition employs data available at a given time in perceptual space. This does not correspond to a single time in retinal or object space. This variation in object time is fodder for the magician and the defense lawyer. Man does not perceive all of the activity in a scene at the same time, even in the absence of a requirement for an optokinetic response. However, his initial perception associated only with threat perception, occurs prior to much of the additional signal processing required for perceptual evaluation and cognition. It is the result of these initial perceptual actions that are required to be transmitted back to the super colliculus as soon as possible.

Boussaoud, Desimone & Ungerleider provide considerable topographic information concerning the temporal lobes of the CNS in monkey13. However, they do not discuss the topology of the temporal lobe or its role in developing interps and percepts. They do not discuss any signal paths between the temporal lobes and the frontal lobes.

Milner & Goodale14, and Milner15 have recently written on the modularity of the CNS, particularly with respect to visual awareness. Like so many others, they have found a dichotomy in the operation of the CNS. Their dichotomy involves the visual portion of the cerebral cortex described by a (conventional) dorsal signal path and a ventral (alternately temporal) signal path. They discuss “covert vision” (blindsight) in the context of the ventral path but does not discuss the potential of the thalamus to explain blindsight and many other equally important performance characteristics. They do not address any saliency map or the detailed operation of their ventral path in the generation of interps and percepts.

Based on the above discussion, the role of the posterior portions of the cerebral cortex can be examined from the perspective of their functional roles. It is interesting to note that one of the major roles associated with threat detection involves the generation of the large saccadic motions associated with the optokinetic response. For a threat that is already imaged on the foveola, no large saccadic response is required. Therefore, it can be said that the signals from the foveola need not be processed in the same manner as those associated with the peripheral retina, and they are not. Alternately, the signals from the peripheral retina are not of sufficient spatial resolution to support effective perception of the threat. Therefore, it can be said that the spatial correlates of the peripheral retina found in the cerebral cortex are needed to support the generation of large saccades, to bring the image of the threat into the foveola, but are not required to support threat evaluation. This would suggest that the areas V1, V2, V3 and V4 contribute signals to the super colliculus to create the large saccades, and they do. It also suggests that they are not required to provide detailed information in the spatial coordinates of the retina to the higher levels of perception, and they do not. This information is provided to the higher numbered levels by the pulvinar pathway (discussed below).

Robinson, et. al. defined a series of neuron types within the posterior parietal region based on the functional nature of their discharge (action potential) pattern. These include:

+ Saccade neurons that discharge prior to visually guided saccadic eye movements.

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+ Visual fixation neurons that fire tonically while the monkey gazes at a target light. Two sub-types were noted.

+ Tracking neurons that become active while the monkey pursues a spot of light moving slowly in one direction. These cells are direction of motion sensitive.

+ Hand projection neurons that discharge prior to visually guided reaching movements and are responsive to passive visual and/or somatosensory stimulation. There are subtypes.

These neuron types appear to be useful in evaluating the performance and architectural significance of the posterior parietal region.

### 15.1.1 Brief overview: the human visual system is different

In developing this chapter, one fact became abundantly clear concerning vision. It is in the operation of the diencephalon of the paleo-cortex where humans differ most significantly from the other primates. It also became clear that this is the least understood of the cortical bodies. The term terra incognita has been used to describe this area even during the late 1990's.

The diencephalon is dominated by the thalamus, that is also poorly understood from an operational perspective. The thalamus is enshrouded by a structure known as the thalamic reticular nucleus (TRN). This structure has not been discussed in the vision literature at all and is under-represented in the brain literature. It is the key to the operation of the primate nervous system. Taylor has discussed this potentiality\(^\text{16}\). More significantly, the TRN is only developed to its fullest extent in the human species. When the perigeniculate nucleus of this structure is combined with the posterior portion of the pulvinar, to form the perigeniculate/pulvinar couple, that the unique visual capabilities of the human are obtained. It is the operational activity of the perigeniculate/pulvinar couple that gives humans the ability to analyze fine detail and to read.

Because of the above findings, this chapter will be presented in two major sections. Sections 15.1 through 15.4 will be presented within a conventional context compatible with the vision literature. It will surface but not explore several major gaps in our understanding of the visual system circa the mid 1990's. The gaps will be centered on the role of the lookup tables (or other structures) required to implement the feature extraction mechanisms so critical to human vision.

Sections 15.5 on will reprise the earlier material, review the operational goal of the visual system, provide significant new material on the role of the PGN/pulvinar couple, and lead into a discussion of the unique ability of humans to analyze fine detail and read. Section 15.6.4 will provide a newer set of schematics, diagrams and flow charts related specifically to human vision. These supercede the more generic figures found earlier in the chapter.

A major theme will be that the use of the lower primates at the frontier of vision research is no longer a viable option. Their systems are not representative of the human system.

A brief summary of the discussion to follow is appropriate. The visually oriented portion of the brain consists of a large distributed group of modular feature extraction engines (also known as sensory association areas) that may also contain memory and that operate asynchronously. The retina is connected to the old brain initially by the optic nerve. This nerve trifurcates into three principle pathways that can be labeled according to their functional capability.

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+ The S-pathway, or summation pathway (also known generically and historically as the M-pathway), delivers a majority of the luminance information to the cortex via the magnocellular portion of the LGN. The signals carried over this pathway are the R-channel signals of this work.

+ The D-pathway, or difference pathway (also known generically and historically as the P-pathway), delivers all signals encoded as differences. These signals include the two chrominance signal channels, any appearance channels (more important in non-primate chordates) and the polarization channels in some animals. The D-pathway parallels the S-pathway but proceeds from the retina to the cortex via the parvocellular portion of the LGN. In humans, this pathway carries the P- & Q-channel signals.

+ The S’-pathway, an auxiliary summation pathway, is found only in animals with significant foveas. This third pathway is recognized morphologically in the literature. However, there is little material on its functional significance. This path provides a direct connection between the photoreceptors of the foveola and specific feature extraction engines of the cortex without passing through the LGN. The path is via the PGN to area V5 (labeled area 7 in this work) of the cortex. The portion of the path from the foveola to the PGN is part of a servo loop used to extract information from the imaged scene in considerably higher resolution than that conveyed over the S- and D-pathways. This servo loop controls the oculomotor system in conjunction with the vestibular system and a perturbation generator that has not been recognized morphologically. This servo loop introduces both the saccades and the tremor associated with the eye of higher chordates. The tremor is the mechanism for converting the signals from the change detectors of the eye into an image for feature extraction in the cortex. The signals from the foveola carried over this pathway are labeled Y-signals in cats and correspond to the S-, M- & L-channel signals as a group.

There is growing evidence in the literature that suggests the cerebellum plays a major role in the vision of the higher primates. However, the detailed definition of that role will only appear in PART II of this chapter. In this work, the term interp will be used to describe a vector signal created by the PGN/pulvinar couple as part of its responsibilities within the Precision Optical System associated with the old brain. An interp is the interpretation of the symbols presented to the foveola during a nominally 50 ms interval within a gaze of about 220 ms. The cerebellum may be the large and primary lookup table that stores virtually all previous interps created by the PGN/pulvinar couple during a major part of the life of the subject. When presented with an interp, or series of interps, it issues a corresponding percept that can be passed directly to area 7 of the cerebral cortex. The percept is also a vector signal that represents a nominal description of what is imaged on the foveola. Both interps and percepts are expressed in a symbolic machine language that is currently unknown. This language is abstract. It is entirely non-visuotopic.

The importance of the S’-pathway, the PGN and the pulvinar pathway to area 7 introduce a problem with the label “primary visual cortex” used to describe the posterior portion of the occipital lobe of the cerebral cortex (see Section 1.2.3). As discussed in Section 15.2.5.3.5, the most important visual information of all does not pass through this structure. Therefore, the descriptor “primary” may not be appropriate. Because of the dispersed nature of the visual system within the cranial cavity, even the descriptor secondary may not be appropriate.

It appears the path through the occipital lobe represented by areas 17, 18, 19 up through 22 (V1, V2, V4, V5, etc) are involved primarily in the preparation of information from the peripheral retina for cognition. It does this by sequentially eliminating the correlation of the information with the retinal image in favor of a more abstract vector notation.

Little or no information is available concerning the mechanisms of cognition following feature extraction at the perceptual level represented by areas V2, V4 & V5 as a minimum. With additional information being gathered daily via PET and MRI scanning techniques, there is a growing belief that each feature extraction engine, numbering in the thousands, includes a memory component. This suggests that each feature extraction engine is a complete entity within itself concerning a specific feature and that cognition may involve a collegial sharing of the output of the individual feature engines.
As noted below, the engines of the occipital lobe operate asynchronously for several reasons. The signals are generated with different delays in stage 1 by the photoreceptors of the retina, the signals encounter different delays in passing through the signal manipulations of stage 2, the signals are delivered with asymmetrical delays by stage 3 and involve different transport delays based on their point of origin in the retina (compensated for by Meyer’s loop in the case of non-foveal signals), and the individual engines involve different amounts of signal processing which also introduces small delays. The difference in the above delays can be significant between signal paths. As an example, they are believed to introduce delay differences between the chromatic and form sensing engines of 50-100 ms.

The situation is different with regard to the signals from the foveola. These signals are processed synchronously by the PGN and the rest of the POS.

At the current time, little is known about the topology and/or topography of memory. It is generally discussed conceptually as containing three or four major components, at least one of which is distributed and associated with the individual feature extraction engines. Pansky, et. al\(^7\) describes memory in two major categories, short and long term and then subdivides each of these two categories into two more; sensory and primary as well as secondary and tertiary respectively. The personal experience of this author conflicts substantially with the characteristics they assign to sensory memory. Nolte has provided another table of memory types and noted the disparity in nomenclature within the field and the speculative nature of the labels\(^18\).

Fuster has discussed his position on memory in a detailed introduction\(^19\). He hypothesizes a memory element associated with every functional area of the brain. The memory associated with a specific functional element may be uniquely tailored.

This work will generally support the idea of a widely distributed memory system. It also supports a variety of memory types. However, there may be a dominant memory element that will be defined in this work as the saliency map. The vector information arriving at area 7 via the Pulvinar Pathway, and via the occipital lobe appears to be assembled (along with the data from other sensory systems) in this saliency map. This map describes the environment (both external and internal) faced by the organism. It is this saliency map that the higher cognitive centers can rely upon and access for purposes of cognition. It offers both current and historical saliency information.

This work will also define in some detail a unique multi-plane two-dimensional associative memory used in the interpretation and perception mechanisms.

[See Section 15.5 for additional comments on the material in the later parts of this Chapter.]

15.1.1.1 Major sources in the literature

The monumental work in 14 volumes, Cerebral Cortex, (begun in 1984 with latest volume in 1997) must be considered the most comprehensive work on the brain\(^20\). However, it is becoming quite dated and contains virtually no information on the operation of the neuron or on signaling within the neural system. Except for the last few volumes, it predates the more recent radiographic, MRI, fMRI, PET and other techniques\(^21\). The preface to volume 12 provides an interesting monologue concerning the dissidence in terminology within the field. More current books
The recent paper by Crick & Koch defines the rapid changes in the common wisdom occurring at present\textsuperscript{22}. Their comments concerning conscious visual representation (perception in this work) and the “primary visual cortex” (or V1) are quite illuminating.

“We have argued that in primates, contrary to most received opinion, it is not located in cortical area V1... This is not to say that what goes on in V1 is not important, and indeed may be crucial, for most forms of vivid visual awareness. What we suggest is that the neural activity there is not directly correlated with what is seen.”

They also describe the evolving concept of an on-line system and a seeing system within the visual system. While approaching from a different perspective, it appears the on-line system corresponds to the analytical channel of this work. The seeing system appears to correspond to the awareness channel.

Young has provided considerable material on the morphology of the cortex of \textit{Mollusca}. There are a variety of good works on the morphology of the cortex in \textit{Chordata}. The emphasis here will be on processing in \textit{Chordata}. Rodieck\textsuperscript{23} prepared a comprehensive review in this area, primarily relating to cat, in 1979. He has recently prepared a new textbook on the operation of the eye with very valuable information on the morphology and topology of the initial signal processing within the brain\textsuperscript{24}. The broadest range of investigation of the cortex has been by Zeki and his associates at University College London. This activity is still ongoing. Several of their works will be referenced below.

In any analyses of the cortex, the volume of work by Noback\textsuperscript{25} should not be overlooked. The illustrations by Demarest in that work are superb. The current introductory text by Kandel, et. al\textsuperscript{26} contains a great deal of material on the detailed morphology of the cortex but it is a fourth edition (the third was in 1991). It is important to know how much new material is included and how much is outdated. As in many other texts, this work takes the position that much of the data is useful but most of the concepts are dated. In one area, it describes the topology of the cortex based on a very comprehensive review by Merigan & Maunsell\textsuperscript{27} as well as other results emanating from recent PET and MRI analyses. Kandel, et. al. may have advanced the work of Merigan & Maunsell farther than appropriate through artistic means in one area. The PET and MRI analyses are beginning to illuminate the interior space of the cortex more than available by probing from the exterior. This work will review the possible organization of the signal paths within the cortex. One community is currently in heated discussion concerning whether there are parallel signal pathways in the brain (possibly) replicating the putative parallel pathways in the optic nerve. An important aspect of the question of parallel paths is, “where do they lead to?” A second question is “are the paths parallel in topological space or topographic space?” One of the modifications by Kandel, et. al. is to show a clearly topological figure of Merigan & Maunsell in a topographic context (using a curved perspective suggestive of the surface of the brain). This general concept appeared earlier in the 3\textsuperscript{rd} edition of Kandel, et. al. in 1991 and in a series of papers by Livingstone & Hubel in 1988\textsuperscript{28}, 87 & 84. Their work followed that of Rodieck with the cat mentioned above. The possible alternative path arrangements, based on the architecture suggested by computer science and other aspects of signal (or cargo) traffic management, will be reviewed. An additional source is that of Nolte &

\textsuperscript{27}Merigan, W. & Maunsell, J. (1993) How parallel are the primate visual pathways
Angevine\textsuperscript{29}. This text is distinct from the Nolte text referenced above.

Carpenter & Sutin provide a well known reference on Human Neuroanatomy\textsuperscript{30}. It includes a number of color plates related to the visual system. However, it does not address the detailed operation of the visual system. Most neuroanatomy texts do not even reference tremor with respect to the oculomotor system.

Two recent works are particularly important in understanding the operation of the visual system. Steriade, et. al. have provided a two volume set on the Thalamus\textsuperscript{31}. It will be shown that the thalamus, not the primary visual cortex, is actually the center of the visual system in animals. Sherman & Guillery have provided a comprehensive volume focused on the gross signal paths of the thalamus, with particular emphasis on the thalamic reticular nucleus\textsuperscript{32}. It will be shown that it is this element that is the major controller of the visual and other neural signal processing activity in the CNS.

Hung & Ciuffreda have recently provided a compendium containing material on the neural system associated with visual cortex\textsuperscript{33}. However, the material is aimed at an introductory level.

15.1.1.2 Subdivision of the neural system into functional stages

When discussing the functional organization of the visual system, the subject of the autonomous nervous system and its subdivisions arises. The clearest definition of this system appears in Chapter 19 of Miller & Newman by Skarf\textsuperscript{34}. He begins by addressing the three types of neural structures [sic] afferent, efferent and central integrating structures, that are included in the vegetative or autonomic nervous system. In this work, the latter will be related to the cognitive and command generation tasks of the visual system.

Synopsizing his definition of the autonomic system, “Body functions that can proceed independently of volitional activity are regulated, at least in part, by reflex mechanisms. . . included in the vegetative or autonomic nervous system. The traditional classification of the autonomic system into sympathetic and parasympathetic divisions is not entirely satisfactory, because such a classification is based primarily upon an anatomic subdivision and not upon a functional differentiation according to activity.

Viewed broadly, the autonomic system ensures self-preservation of the organism by making continuous automatic adjustments so as to maintain homeostasis in the face of major and minor environmental changes. Sympathetic and parasympathetic elements in this system act, in a balanced fashion, to maintain homeostasis. . . Sympathetic activity mobilizes mechanisms of the body to meet conditions of stress: . . . Parasympathetic activity has an opposite function, that of conservation and restoration of bodily resources.” The dilation of the pupils is considered sympathetic and the constriction of the pupils is considered parasympathetic. This is interesting since both actions are controlled by a single neuron-muscle servomechanism.

Quoting further, “The term ‘limbic system’ was applied to several areas with the central nervous system (CNS) that are associated with autonomic functions.” After much discussion of its potential constituents, he summarizes, “Thus, the concept of a limbic system is a tenuous one, and its definition and use remain controversial. Indeed, Brodal (1981) argued that the term should be abandoned.”

\textsuperscript{30}Carpenter, M. & Sutin, J. (1983) Human Neuroanatomy, 8\textsuperscript{th} ed. Baltimore, MD: Williams & Wilkins
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He concludes a section on the role of the cerebellum with “The significance of this cerebellar autonomic representation is not fully understood.” This position is quoted because of the material developed in this chapter is aimed at defining its representation.

15.1.1.3 Subdivision of the cortical system into functional stages

This work will continue to separate the primary functional responsibilities of the brain into:

- stage 4–perception
- stage 5–cognition
- stage 6–command generation
- other–abstract thought and other processes

In the context of this work, the cortex is primarily concerned with stage 4 activities but must accommodate certain stage 3 activities within its morphology. The stage 3 activities include the decompressing, through one level of decoding, and recovery of the signals presented to the input structures of the ganglion cells of the retina. This decoding completes the functions of the projection stage. The data is then turned over to the remainder of the cortex for further perceptual processing prior to cognition. Realization of this decoding roll places a larger responsibility on the LGN than indicated by Merigan & Maunsell. There are approximately ten times as many neurons leaving the LGN, in the optical radiation, than enter it from the optic nerve. They describe that responsibility as the relay of signals from the two pathways (M and P pathways) to the cerebral cortex. This work also complicates the problem of interpretation of the input structures of the brain. It demonstrates that the M and P pathways are not monolithic individually. The M pathway is particularly non-homogeneous and the so-called P pathway bifurcates before it reaches the LGN. And the reader should carefully note the conflict in terminology concerning the letters M & P presented in the introductory material of PART D. New terminology will be suggested in this area. The occipital cortex may also accommodate stage 5 activities but the nature of these is still virtually unknown.

The discussion of memory generally leads to the conclusion that it appears in several distinct categories that cannot be associated exclusively with one of the above stages.

Zeki and Marini have suggested a subdivision of stage 4 into three substages. The suggestion that there may be three substages appears useful. However, this work would define these substages quite differently. The following detailing of these stages is the responsibility of this author. The first substage can be defined as involving the spatial registration of luminance, chrominance and appearance information. Activity of this type is concentrated in the LGN, V1 and V2. Only limited information extraction is performed in these areas, primarily related to initial threat determination and signal generation impacting an optokinetic response by the super colliculus and the AOS. The second substage will be defined here as involving the initial perception of the threat, and only the limited amount of perceptual evaluation required to support a maximally precise total optokinetic response by the organism. This function is believed to occur primarily in V4. The third substage will be defined as higher level perception. This level of perception involves complete feature extraction from the incident signal information, probable storage in local memory of this data in engram (vector form), and probable transmission of this data, or addressing information relative to this data, to the cognitive centers of stage 5.

15.1.1.3.1 Interpretation

The initial processing of signals received over the optic nerve leads to what will be called interpretation in this work. It occurs primarily in the mid brain and is accomplished as rapidly as possible for two reasons. To respond to threats to the subject as quickly as possible, and to perform as much initial analysis leading to an interp as possible in the limited time available.
In this work, interpretation involves the initial analyses of the signal vectors delivered to the old brain from the eye and other organs. At this level, there is sufficient data (one or a very few interps) available for the animal to take evasive (more generally responsive) action if appropriate. However, it will not “know” why it did so. Knowing requires additional perception followed by cognition (terms to be defined below). Only in retrospect will a human be able to say what action he took and what environment he faced at the time.

The performance of a baseball batter or other athlete is an excellent example of this situation. If you ask a batter how he knew to swing low, and how he made the decision in much less time than the psychologists say is possible, the batter will say he does not know. He only knows that he can get paid very well for repeatedly doing it correctly.

There is no substantial signal storage capacity in the retina, particularly in human unless it is rudimentary in the 2nd lateral processing matrix. It appears necessary for the system to provide some sort of short term memory at the input to the cortical structures to accumulate data from the essentially serial collection process of the retina. This is particularly true with regard to the foveola where the data is generated in very small increments during a 30 ms time interval.

15.1.1.3.2 Perception

The next level of analyses involves the perception of the received data. Perception, as used here, involves the analyses of an interp or group of interps and forming a percept. The percept is a message in vector form that is transmitted to area 7 of the cerebral cortex where it can be integrated with other percepts describing the environment of the subject.

This conversion of interps into percepts (both in vector form) results in a great reduction in the data volume required to be transmitted to the cerebral cortex without obvious loss in information content (from the animals perspective). This function appears to be performed by additional “function extraction engines” associated with the old brain. The individual processes performed within these engines are beyond the scope of this work.

This second level of perception is a much more complex and memory intensive process than the initial collection of data over multiples of 30 ms described above. It leads to awareness of the environment and willful action based on this awareness. It is also the only area of the visual system that is clearly dependent on closed external feedback loops. Guyton35 has provided a neural map of the pathways controlling the movement of the eyes. More recently, Oyster36 has provided valuable information on the morphology of these channels.

One of the principle tasks of the initial higher level processing is to eliminate as much as 99% of the data so carefully preserved by the earlier signal manipulations. This allows the system to concentrate on the further processing of data signals containing a higher percentage of information in the Shannon sense. It is proposed that this level of processing occurs in an abstract signal (vector) space, not in a space representing a literal transposition of the image on the retina to an equivalent space within the brain. There is no little green man back there to look at such an image. Any morphological mapping between the far field image and the surface of the so-called primary visual cortex is at the crudest level. This large scale mapping fails completely by the arrival of the signal at the feature extraction engines as demonstrated by recent PET and MRI scanning results. Signals appearing at the output of an extraction engine will be labeled an abstract vector or, an engram.

15.1.1.3.3 Cognition EMPTY

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**15.1.1.3.4 Distribution is key to the operation of the brain**

It is unfortunate that Rodieck disdains the use of the signaling channels concept on page 269 of his most recent book although he employs it again later, at least on page 322\(^{37}\). This work will show that the problem consists of two parts. First is that he has not (at least on page 269) accepted the concept of sub-channels (or multiple parallel channels). In this work, a single channel is frequently described that is meant to be prototypical of thousands or millions of similar channels found throughout the retina and brain. These channels may converge significantly as part of the overall encoding process, only to diverge again within the cortex as part of the decoding process. In between the convergence and divergence functions, it may be extremely difficult for the electrophysiologist to track an individual signal. However, the channel is still there. It is just that to describe it requires a very complex notation involving temporal, spatial and diversity encoding nomenclature (and more sophisticated instrumentation). It is like trying to definitively describe the path followed by a packet sent over the INTERNET, a system designed to be highly reliable and highly independent of individual signal paths. Such a system can suffer the loss of innumerable individual neurons without significantly affecting overall performance.

Second, he has not recognized that the various types of ganglion cells exist because they are optimized to support a particular signal environment, not a particular signal class anticipated by an investigator. His argument is couched in terms of the problem of midget ganglion cells and other ganglion cell types projecting to more than one place in the brain. The same type of ganglion cell optimized for encoding biphasic signals can be employed in any signal channel (or sub-channel) required to project biphasic signals. He draws the conclusion that: “Ironically, the activities of the two groups of ganglion cells specialized to signal the direction of motion appear to make no direct contribution to conscious visual perception.” *Emphasis added.* This statement is true. The word conscious is key to its validity. Whether the situation is ironic or not is another question. A premise of this work is that visual signal paths can be decoded and analyzed in the brain at locations involved in perception, a sub-conscious function, prior to their being decoded and analyzed for purposes of recognition, a conscious function. Recognition is a conscious result of higher level analyses that has little to do with the type of projection neurons used to deliver the signals to an earlier analytical function. The use of signal channels to describe the operation of the visual system will be continued here because of the valuable insights provided if the model is adequate. Rodieck does discuss the fact that some ganglion cells send their axons to both the superior colliculus and the LGN (page 322). This Chapter will suggest the axons more often went to both the PGN and the LGN. It is proposed that these signals undergo considerable manipulation and modification between the PGN and the superior colliculus.

**15.1.1.3.5 Tremor is key to the operation of the visual system**

One of the difficulties in Rodieck’s 1998 book is that it does not address the importance of tremor in the visual process. (Neither does Kandel, et. al. or many others. Although Rodieck’s book stresses the fact the visual system is blind in the absence of motion of the line of sight relative to the scene, it concentrates on the relatively coarse motion imparted by the saccadic and skeletal motions of the animal. This work will delve a bit deeper without crossing into the recognition arena. It will show that the visual system operates in at least two separate and distinct initial signal analysis modes leading to perception. These modes do not negate the value in speaking of channels. They merely require that the utilization of the channels by the initial analysis circuits may be a function of the animal’s situation within the ecological environment.

Tremor is the fundamental mechanism employed by the POS to both control the line of sight with precision and to perform the initial cross correlation on the image presented to the foveola.

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Another difficulty found throughout much of the literature relates to the appearance of signals from various spectral types of photoreceptors in the neurons of the LGN and beyond. The authors frequently do not indicate the nature of these signals in sufficient detail to avoid ambiguity in the context of this work.

A difficulty shared by many investigators is the continued use of the adjective ON-OFF or the adjective ON-Direction to describe the operating mode of an analog biphasic signal. It has been similarly applied to the output of ganglion cells encoding these biphasic signals. The underlying analog signals are not well represented by this archaic nomenclature. The encoded action potential pulse stream created by the ganglion cells from these signals does not represent an ON-OFF transition under normal operating conditions. This type of performance is only found at extreme stimulus levels where such performance is indicative of saturation in the system. Unfortunately, many laboratory investigators employ saturating optical signals to simplify their experiment design.

When encoding a biphasic signal related to a change in illumination between an adjacent pair of photoreceptors, which can be related to motion in the visual field when the signals from a group of such pairs is analyzed, the mode of signal encoding in vision does attach a preference to signals of one polarity. This frequently accounts for the observation that the response of an animal to an advancing bright border is more pronounced than the response to an advancing dark border.

A semantic device appears unusually frequently when reviewing the literature of the brain. Several authors have remarked that results were counter-intuitive. It is not clear how intuition is supposed to be used within the scientific method, except possibly in stating an initial premise during experimental design.

15.1.3.4 Stereopsis

This chapter will not discuss stereoscopic vision. Several texts explore what is known in this area.

15.1.2 Background

It is a very early day in the understanding of the operation of the brain in both perception and cognition. A recent comprehensive text on the human brain has a subtitle of “An introduction to its functional anatomy.” From the perspective of this work, it only addresses gross anatomy based on topology derived from morphology and behavioral characteristics based on anomalous behavior as a result of injury or surgical intervention. It contains very little on function related to signaling, devoting only one sixth of a page to cognition (0.02%), less than four pages in 600 to memory (0.6%), and does not address the subject of perception in the index. A relatively recent comprehensive review of neuroscience devotes two pages in 576 (0.3%) to a highly conceptual flow diagram of memory and memory processing, and does not address the subjects of perception or cognition in its index.

This work has uncovered considerable research data showing the brain is quite different from what is normally depicted in vision research documents. The fact that there are nearly as many neural paths from the striate cortex back to the diencephalon as there are neural paths from the diencephalon to the striate cortex suggests the striate cortex is an auxiliary element relative to the diencephalon and not a major element in its own right as usually depicted. The conclusion is that the diencephalon contains the “control point” for virtually all high level neural activity and that the pulvinar, cerebellum and occipital lobe of the cerebrum are members of a hierarchal group of correlation elements supporting the cognitive and motor centers via the control point. The control point appears to be the seldom discussed outer shell of the thalamus, known as the thalamic reticular nucleus. [xxx see Taylor citation above ] The thalamic reticular nucleus appears to work in close cooperation with the limbic system to establish,
control and display the emotional state of the organism.

15.1.2.1 Anatomy

The study of the anatomy and morphology of the brain is an old science. However, because of cultural constraints, amazingly few human brains have been studied in detail. Up through at least the end of the 1980's, the brain was still studied from the perspective of “form dictates function.” This dictate is difficult to understand. It appears that it was followed by the biological community primarily due to its enthronement by the educational system. Such a proposition is probably unknown in other sciences. Another basic premise has been that the brain was organized into discrete regions where all activity of a given type was focused. This latter proposition has finally given away to the understanding that the brain is a distributed set of modular functional areas, no one of which controls all of the functions related to a given sensory input or motor output.

If one takes the opposite view from “form dictates function,” that form follows function, it becomes possible to discuss the anatomy of the brain in a more conventional scientific, and engineering, sense. One can define the operational requirements, the available packaging space, the available power sources, etc. and then draw up the likely or even preferred implementation. A particularly important requirement is introduced by the relatively slow transit velocity of neural signals. In the case of the chordate brain, three primary requirements are; minimum distances between the principle sensory organs and the analytical centers of the brain, minimum total volume in order to maintain a minimum moment of inertia relative to the remainder of the organism, and maximum physical protection because of the exposed location of the organ at the front of a highly mobile structure.

In the case of the primates, the above requirements still exist in spite of the requirement to increase the total amount of volume devoted to signal manipulation. An additional requirement is based on the limited ability of neurons to transmit signals over long distances (measured in millimeters) in analog form. For longer distances, it has been found necessary to employ pulse transmission methods and to employ regenerative repeaters at regular intervals. This practical limitation has a profound impact on the true functional organization of the brain. It suggests that a nominal volume for a discrete processing function, an “engine” as defined below, is about 2 x 2 x 2 mm in volume (see next section). It is important that each such volume have excellent communications access to other similar volumes and that it be adequately supplied metabolically. These requirements suggest a thin membrane immersed in a nutrient environment with extensive interconnections (on the inside to minimize distance and therefore signal travel time). But to maximize the usable volume within a fundamentally two dimensional structure that must be enclosed inside a minimum volume case, it is optimum to crenalate the surface of the structure as much as possible. This is exactly what has occurred, particularly with regard to the neocortex, i. e., the new brain introduces as an add-on to, or expansion of, the old more limited capability brain.

15.1.2.1.1 The three morphological types of brain and their relative neural power

The various portions of the brain have developed in startlingly different physical ways. The old brain began as merely a grouping of neurons at the end of a central conduit containing many neurons. It was just a major node. As evolution continued, the diencephalon became a bulbous solid three-dimensional mass of neurons at the end of this central conduit. Communications within such a solid volume, limited largely to tonic signaling, became difficult and several internal “lamina” were introduced. The more important change was that stage 3 signaling via short commissure were used between these bulk structures. As the new limit, provided by this approach, was reached, a new approach became necessary. The cerebellum was introduced. It is a highly folded but relatively thick structure, in terms of equivalent neurons between the inside and outside surface. This structure provided a great deal more

interconnection capability while still providing a significant correlation capability over spans of many neurons. As the need for a still greater degree of interconnection was needed, the cerebral hemispheres were introduced. These structures are essentially paper thin. They are typically described in terms of about six identifiable layers of neurons with a total thickness similar to that of the retina, 500 microns or 0.5 mm. To minimize the length of the commissure between engines, the surface is highly crenelated.

It is convenient to treat each of these types of brain separately and calculate a nominal number of standard size neurons within a unit volume for each type of brain. For discussion, take the standard size of a neuron as a 10 micron diameter sphere on 10 micron centers (with no limitation on the number or length of neurites or axons extending from this volume. For the thalamus of the diencephalon, a bulk structure, a 2 x 2 x 2 mm mass would contain approximately eight million neurons. Assuming two neurons to a circuit element equivalent to a two state flip-flop, this is approximately the memory capacity equivalent to about four megabits of RAM in a PC. There is a problem of terminology here. The computer industry speaks of RAM in terms of an 8-bit word as one byte. Thus four megabits of RAM is equivalent to 0.5 megabites of RAM. If this circuit capacity were devoted to computation instead of memory, it would be roughly equivalent to the computing power of a modern PENTIUM IV microcircuit.

For a thinner structure, such as the cerebellum or the cerebral hemispheres, such equivalent neural volumes would require greater surface area. In the case of the cerebral hemispheres, with a thickness of 0.5 mm, a surface area of about 4 x 4 mm would be required to provide eight million neurons. This is the approximate computing power of a PENTIUM IV microcomputer chip. The cerebellum is generally thicker than the cerebral hemispheres but less than two mm thick. It would require an area intermediate value compared to the earlier values to achieve the same capacity.

15.1.2.1.2 The sheet form used in the cerebral hemispheres

Most discussions of the brain focus on the cerebral hemispheres because of their physical prominence, and the fact they effectively hide the other large structures.

The reader is cautioned that the word architectonics has been used since the 1920's in the study of the anatomy of the cerebral hemispheres. The roots are those used in geology to describe the study of a surface. It is distinctly different from the more specific term, plate tectonics, that involves the inter-relationships between discrete large regions of a surface (however, the anatomist has clearly thought in similar terms). Originally, the anatomists looked to the interconnections of the areas circumscribed by sulci. They did this be tracing the paths of myelinated neurons and the term myeloarchitectonics appeared. A second school took a different approach and studied the difference in the morphology of the neurons in these different areas. This generated the term cytoarchitectonics. Neither of these approaches has led to a understanding of the operation of the brain at a detailed level.

The literature has long studied the surface configuration of the brain from the perspective that each region circumscribed by fissures (called sulci) was functionally independent. This concept began breaking down in the middle of the 20th Century with the introduction of several techniques allowing the tracing of the terminal points of individual commissure. It was found that the surface area within the fissures was just as important functionally as the outer surface areas. Many 4 x 4 mm size areas can be placed completely within a sulci.

The reader is also reminded of the discussion in Hamilton on the subject of ablation as a means of studying the operation of the brain and determine the seat of a particular function within the brain. He stated42: “A point of logic regarding the ablation method is so simple that it deserves mention only because it is so frequently overlooked. The rhetoric is awkward, but one does not study the effects of a lesion–one studies the ability of the remaining brain

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tissue to control behavior.”

Hamilton’s Preface outlines a wide variety of problems found in the field of cortical anatomy. Two of the most difficult are the wide variety of overlapping terminologies used and the profusion of labels used to define different areas of the brain. The terminology employed has never been subject to a rigorous standardization procedure within the label “central nervous system,” nor has it been standardized in conjunction with the “peripheral nervous system.” Hamilton reviews the duplication and conflicts in this area. It is so confused that Hamilton quoted Riggs citing a humorous recital by Wald. Figures 114 and 116 of Bailey and von Bonin illustrate the problem well. Those authors credit the author of figure 116 with a valiant effort.

In attempting to map the cerebral hemispheres (and other areas of the brain), the problem is that it is a continuous functional medium, instead of consisting of discrete areas or volumes. As a result the problem of defining the functional areas of the brain is difficult, to date unmanageable. Immediately prior to introducing their own (less than precisely defined) map, Bailey and von Bonin said: “The subject became not only difficult and abstruse, but doubts about the reliability of cytoarchitectonics grew until, ‘Unless the criteria are clearly stated and objectively verifiable... architectonic charts of the cortex represent little more that the whim of the individual student,’ could be written, amidst widespread applause, by Lashley and Clark (1946).” They also noted on page viii, “Anybody can see the difference between Brodmann’s areas 17 and 18. But the differences between his 18 and 19 are quite tenuous and very difficult to recognize. To draw a map on which these three areas are given three different markings—such as dots, cross-hatchings, and broken lines—is to create an entirely misleading impression.”

The structural uniformity of the multilayer laminate known as the cerebral cortex is so high that its surface is generally considered translationally symmetrical, although there may be an exception in areas involving spatial correlation. In the latter areas, long neurites and axons are found coursing along individual laminates near the surface. The result is a reticulated appearance in these areas.

The Bailey & von Bonin book provides an excellent source for nearly all of the morphological maps of the cortex to date, except their own in 1952, and much other information on the cortex. However, the reader is cautioned that they reiterate their conviction that structure determines function. Such a position is really only tenable at the quantum molecular level where the function of the Activa is in fact determined by form and dimension of its base region. They make the interesting statement (a similar one is found in nearly every treatise on the brain) “The architectonic types are described first, although the method of induction would demand them to be put last.” The fact is the architectonic types could be omitted except for providing general landmarks. It appears that a few of the major (primary) sulci are species specific across racial and other lines. However, the more local sulci are quite variable between individuals and the result of local variations in packaging. They also note the occipital lobe has been the most difficult to analyze morphologically, especially along the lateral sides. This appears to be an overstatement when compared to the cerebellum.

While housed in a container that allots only about one half of its total volume to the brain, the cerebral cortex has a surface area of about 2,400 sq. cm. (for males) but an exposed area of only about 600 sq. cm. If a new mapping be accomplished using the capabilities of the computer to prepare a flat map of the cerebral cortex based on a wire frame model of a nominal brain. To avoid the variations due to packaging noted above, the map should have the origin of the brain associated with it, possibly “the Brain of the Unknown Subject.” Bailey and von Bonin labeled their brain H1.

The literature frequently introduces the concept of a relay station between different parts of the brain or at the interfaces between the peripheral and central nervous systems. Unfortunately, the concept of a relay is usually addressed in causal terms based on the word relay as a verb. In signaling theory, a relay is a device that is capable of performing either, or both, of two main functions, signal regeneration and signal manipulation based on boolean algebra. Based on this work, signal regeneration is accomplished with great reliability by the synapses and Nodes of Ranvier associated with the individual neurons. There is no need for a repeater at the level of a morphological feature. Where significant signal manipulation is involved at a site, this work will suggest that site is of sufficient significance to be labeled an "engine."

15.1.2.1.3 The cerebellum

The functional role of the cerebellum in the neurological system remains largely undocumented. Its role in certain skeletal motion disorders is recognized but even in these cases, the source of the disorder has not been traced to a specific area of the cerebellum. The best that can be said is that disorders of locomotion can be traced to a locus that includes the anterior lobe of the cerebellum. Investigations to date have not defined a relationship between finite areas of the cerebellum and specific body functions. Nolte gave only one paragraph to a discussion of the function of the cerebellum. He suggests it “may be involved in cognition. . . and may play a role in affective and autonomic functions.” In this work, the role is a great deal more important. However, since it is primarily a storehouse of material in a vector format and language that we do not understand, it is difficult to analyze its functions. The new MRI and PET techniques should open a new avenue in this area. Bower & Parsons provided a review of the cerebellum for the layman in 2003. They attempted to define the many functions, including those related to preparing final percepts prior to cognition, of interest in this work.

Blinkov & Glezer have provided a large tabulation of the cerebellum.

15.1.2.1.4 Numbers of neurons, synapses and commissure

The number of neurons in the human brain has been estimated frequently but without a significant degree of precision. An estimate by Economo of $10^{10}$ neurons in the cerebral cortex is probably as good as any. However, Tovee has recently presented a broader set of numbers. He suggests $10^{11}$ neurons, more than $10^{15}$ synapses and at least 2000 miles of axonal connections.

Computing the number of interconnections is difficult without a detailed definition of what constitutes a connection. One estimate of just the neurons in the corpus callosum, connecting the left and right hemispheres, is $10^9$ commissural fibers (neurons). This number would suggest a total number of association neurons of about $10^7$. Such a number would be compatible with the central processor of a modern microcomputer, i. e., about one interconnection with the external circuitry for each 1000 transistors.

In the case of the microcomputer, man has found ways to time share the input and output connections. This has allowed the total number of external connections to a given central processor to be kept below 250 for transistor counts up to tens of millions. However, man has found that this time sharing inevitably slows down the system. To avoid this problem, local memory caches have been incorporated within virtually every central processing chip. By combining central processing units and employing a general software instruction set, he has been able to assimilate hundreds of individual “engines” where each engine contains its own central processing unit and local memory. Such systems still represent a general purpose computer

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capable of being taught to solve nearly any analytical problem, and to make estimates of the solution to non-analytical problems.

After subtracting about $10^7$ synapses from the suggested total of $10^{15}$, one is still left with $10^{15}$ synapses to be divided among the large number of individual signal processing engines of the neocortex. There is no generally agreed number of synapses per neuron, but most investigators would not argue with a number of 1000 within the CNS.

$10^{11}$ neurons could be further subdivided into about 10,000 distinct processing engines of eight million neurons. These would occupy about 0.1 cubic meters based on a solid brain. On a brain of 0.5 mm thickness, the required area would be about sixteen square meters. These numbers suggest one of two things, the typical neuron occupies much less than a 10 micron sphere or there are closer to $10^9$ neurons in the human CNS.

### 15.1.2.2 Operation

Detailed discussion of the operation of the circuits of the brain is entirely missing from the literature. The most that can be found is that the action potentials carried by association neurons or fibers (groups of neurons) have a nominal frequency, may occur in groups of pulses, and may or may not occur at a given location in response to a given stimulus. At a higher level, traffic analysis, generally in conjunction with ablation prior to the introduction of nuclear imaging, has led to some knowledge of the operation of the brain. With the introduction of what is labeled functional nuclear imaging, investigators have been able to ascertain metabolic consumption of different materials as part of the brain's response to a stimulus. However, this activity is highly exploratory at this time and invariably uses excessively complex stimuli. Only with more time consuming analysis with simpler stimuli, will this work begin to quantify the connections between and the responses of different engines of the brain.

The Central Nervous System is organized as a large group of independent asynchronous (also known as clock-less) processors. While man has not yet adopted this type of computer architecture, the concepts involved in this architecture are beginning to be explored in the research laboratories. On the other hand, these independent asynchronous processors are connected by a great number of signal propagation channels that are synchronous. Each of these channels consists of a multitude of individual fibers. The individual channels carry information as serial words made up of parallel bits, just as current computers do. It is the parallel bits that are sent in synchronism with each other. Man has not yet discovered the encoding scheme used to convey the serial word, parallel bit information within even the simplest paths of the brain.

#### 15.1.2.2.1 Signaling architecture

Recent brain research has focused on the great degree of reciprocity in the signals transferred between major elements of the cerebral hemispheres and the rest of the brain. The high degree of reciprocity with regard to the occipital lobe even points to a fundamentally different role for this element. Recent work in learning has also suggested the need for a better understanding of the signals associated with controlling the operation of the brain, in addition to the signaling involved in data processing. Such control signals will be labeled supervisory signals in alignment with conventional communications theory.

It is difficult for the empirical community to rationalize the large variety of signals encountered in the brain without a roadmap or framework. This work will develop a generalized framework and then simplify the framework when it is demonstrated that certain signal paths do not, in fact, exist. The general plan will be to follow the top level block diagram of and the top level signaling diagram of Section 15.2.5. For each of the paths in this figure, initial consideration will be given to the possibility that each of these paths consists of an orthodromic, and antidromic and

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a supervisory signaling subchannel. These paths will become critical to the appropriate understanding of the thalamic reticular nucleus of Sections 15.6.1 & 15.6.2 (in PART II of this Chapter) and in discussions of the learning process in Section 17.8.

15.1.2.2.2 Power consumption

There are a variety of estimates of the power consumption of the human brain. Most of them are based on the rate of oxygen consumption, without regard to any other chemical reactions not involving oxygen directly. McGeer, et. al. provides a brief introduction into this discussion, along with references51. The typical number found in the literature is 20 Watts. The power consumption does not vary with sleep, although it can be lowered by anaesthesia and comas of various kinds. How and where the energy is consumed is still being investigated. It is known that about 80% percent of the blood flow supports the “gray matter,” presumably the unmyelinated neurons composing most of the CNS (by count as opposed to volume), with the rest supporting the “white matter,” presumably the myelinated axons within the commissure. On-going experiments using nuclear isotopes and nuclear imaging techniques are providing more definitive data.

Pellerin & Magistretti have provided a brief discussion focused on energy utilization during the resting condition52. They assert that “while the brain represents only 2% of the body weight (in humans) it contributes up to 20% of its resting metabolism..” They reference Attwell & Laughlin (2001) and conclude “that the vast majority of the energy expenditure (81%) is devoted to neuronal excitatory signalling.” The word excitatory may be superfluous or subject to further discussion. More than 90% of the neurons of the brain are not involved in the generation of phasic signals. The term is usually associated with such phasic signals (action potentials exhibiting a repetitive nature). The term excitatory is easily confused with the term salutatory.

It would be useful to discuss energy consumption under conditions of strenuous mental activity to compare with the baseline resting conditions. The literature has not been searched for such data. However, recent fMRI data has frequently shown 40% increases in local blood flow within the cerebral cortex during even simple mental activities. These studies generally relate cerebral blood flow to glucose consumption.

The literature becomes murky when it discusses positive and negative heat (pg 69 in McGeer, et. al.). These ideas are apparently derived from the energy associated with an action potential followed by an undershoot conceived of as an opposite energy phase by some.

15.1.2.2.3 Timing

No reference or discussion could be found in the literature related to the critical design requirement of timing, either with regard to absolute time delay or to relative timing between the output of various engines.

15.1.2.2.4 Spatial and temporal resolution

Churchland & Sejnowski have provided a useful summary of the spatial and temporal resolution previously achieved using a range of techniques53. Figure 15.1.2-1 extends their figure to differentiate between synapse investigation at the morphological/cytological level and such investigations at the molecular chemistry/crystallography level. The ranges are not meant to indicate theoretical limits. The inclusion of electron microscopy opens a vast area not considered by Churchland & Sejnowski. It allows the definitive description of the synapse and the electrostenolytic mechanism so crucial to understanding the neural system.

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15.1.2.3 Specific themes

15.1.2.3.1 Definition of perception and cognition

Although the complete interpretation of the term perception as used in the psychophysical sciences is beyond the scope of this work, a working definition is required. Uttal has struggled with this term\(^{54}\). He settled for a usage not far from variant 4a in Webster’s Dictionary of 1963. “Perception is the awareness of the elements of the environment through physical sensation or reaction to sensory stimulus.” This definition is too broad for this work.

In this work, a distinction is made between perception and cognition. In general, awareness is associated with cognition. As discussed elsewhere, an animal can perceive a threat and respond to that threat without requiring or employing cognition. In this case, the animal need not be consciously aware of the threat, although he may subsequently become aware of why he jumped out of the way of the approaching car. In this work, perception will be defined as and limited to the reception and initial interpretation (adequate to initiate a motor response) of sensory stimuli related to the elements of the environment.

Cognition will be defined as a higher level state involving the conscious awareness of the elements of the environment and their interpretation within a larger sensory and intellectual environment.

Using these definitions, the animal is capable of responding, through the motor-neuron system based on both willful intent as commanded from the cognitive centers and on inate algorithms designed to protect the animal or to automate lower level stimuli gathering functions such as the tremor employed to evaluate fine detail in foveal imagery.

15.1.2.3.2 Definition of blindness

Historically, blindness has always been defined in terms of a complete loss of vision. The primary deviation from this definition was in the case of color-blindness, a poorly defined concept exhibiting a relatively wide variation in degree. These definitions were in use for ages without the support of current day knowledge of the visual system. In recent times, numerous new subclassifications have appeared in the literature based on clinical evidence obtained as the result of injury, disease, and occasionally surgical intervention. These classifications involve simple form (a subset of appearance) blindness without loss of color perception, blindness to fixed objects within a field, blindness to motion of objects within a field, blindness within the foveola with peripheral vision minimally affected (and the reverse situation), and more sophisticated appearance blindness (failure to recognize faces, text, etc.) without loss of other visual capabilities. These types of blindness have been labeled “blind sight” in the vernacular. The condition of total blindness except with respect to the fovea (or foveola) actually has a generic name, macular sparing. It is encountered in situations where V1 is essentially destroyed but the subject can still read and fixate on objects.

The advent of MRI, PET and CAT imaging techniques have introduced a new age in determining the causes and locations of visual system failure. Prior to this time, the description of a visual failure usually relied upon morphological examination, frequently post mortem, following major damage due to disease or accident. A comparison between a normal and an impaired subject was usually limited to psychophysical evaluation. Recently, Zeki and associates have provided new and detailed information relative to the impact of a visual failure and the resulting changes in the operation of the cortex compared to a normal subject.

Based on the above techniques, an immense amount of new knowledge is now available, some of it correlated for the first time in this work. These conditions require the development of an entirely new set of definitions of complete and partial blindness based on the locations of failures within the top level schematic of vision, both sub-cortical and cortical, developed within this work. Some categories may also require definition based on cortical functions not addressed in this work. These categories and the failure mechanisms related to them will be addressed more fully in Chapter 18.

15.1.2.3.3 Time and space resolution in psychophysics

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Higher Level Perception Pt I 15-  25

Much of the available data in higher level perception has been obtained via psychophysics. While most of the subjects have been “normal” in an un-quantified sense, others have become available to research through the result of accidents. The data that has been collected must be considered primarily exploratory due to the lack of a sufficiently accurate model of the system under test to plan experiments in detail. This has been spectacularly noticeable in the area of determining the optimum illumination for use in a given experiment. It is rare to see a precise definition of the spectral content of the illumination used, much less an actual calibration of that source. The usual practice is to list a manufacturers catalog number for a (typically incandescent) light source and possibly list its nominal wattage.

There are two major problem in interpreting the data collected by these researchers. First, it is rare to find a researcher that is aware of the time frame in which objects or features are actually perceived by the brain (prior to cognition in this context). Second, it is rare to find a researcher that delineates between the operating mode of the fovea and that of the remainder of the retina. Third, it is quite rare for a researcher working in perception to integrate the work of Yarbus and Ditchburn into their discussion. Without considering these parameters in detail, the conclusions that can be drawn from studies of perception are quite limited.

As an example, many experiments are performed to determine the ability of the visual system to respond to a particular feature or shape without determining the detailed eye motions involved in that determination. The impact of eye motion on perception is greatly different for features in the fovea versus features in the periphery of the retina. For the fovea, these motions suggest that much of the perception of vision takes place in a serial time frame of 1/30 of a second per feature (33 ms). The fovea may actually be able to obtain the necessary information to perceive as many as a thousand features in parallel during this interval. The eye then redirects its line of vision and acquires an additional lot of information (from a different scene within the overall scene) in an additional interval of 30 ms. This process is repeated many times. Typically the subject is asked to make a response after either perceiving or recognizing (requiring cognition) a property of the illuminated scene. The choice between perception and recognition is frequently a parameter of the training provided the subject. The difference in overall time delay between these two test conditions can be considerable. Much of this total time delay is a function of the transit time of the signals from the retina to the cortex. Under some conditions, it is also a function of the illumination level used and the contrast level of the image. And frequently it is a function of the precise spectral quality of that illumination. For test objects larger than the projected size of the fovea, the time required for saccadic motions also becomes important.

It is imperative that research oriented experiments either control or measure all of the parameters involved in the above discussion. Otherwise, the results are not repeatable by an independent investigator and not interpretable by any analyst, independent or part of the team. The analytical phase of the investigation should also address the time sequence of the perceptual process in order to understand the subject of serial versus parallel signal processing within the visual system.

15.1.2.3.4 Problems in defining signaling paths, fields of action (maps) and purviews in vision

The literature does not provide a comprehensive, consistent and precise description of the signal paths, fields of action (maps) at different locations along these paths and the resolution and purview of these paths. Nor does it develop the magnification factor between these various characteristics in an organized manner. Part of the problem appears to be the use of the word map. In the vernacular, it suggests a remapping of one plane to another without any definition of the quality or mode of that mapping.

The tone of much of the literature suggests that a reflection of the image projected on the retina is to be preserved throughout the visual system. This is not the case, there is no little “green man” to look at such an image. The goal of the visual system is to extract the essence of the image, the information content of the image and associate that information with other information from other modalities in a saliency map describing the environment (both external and internal) of the organism. Thus, it is to be expected that the maps at various centers of signal processing
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will become less retinotopic and more abstract with distance from the retina. In the vision literature, abstract signals, relating to a given image on the retina but lacking a spatially recognizable form, are usually described as diffuse signals.

The problem of mapping the information from the retina as it progresses through the system has been complicated by a lack of understanding of the two-pathway nature of the signal processing. The information related to the foveola is processed entirely separately from the information from the peripheral retina. It will be shown that the information from the foveola is processed in the perigeniculate nucleus/pulvinar couple while the information from the periphery is processed in the better known lateral geniculate nucleus/occipital lobe couple. Virtually nothing has been reported concerning the more important of these two couples. The perigeniculate nucleus, PGN, and the PGN/pulvinar couple will be a major focus of this work, along with the equally poorly reported Precision Optical System controlling the movements of the eyes relative to the head.

An additional problem concerns where and how the maps are obtained. In general, current electrophysiology techniques only allow maps to be obtained that involve the action potentials associated with commissure, groups of stage 3 projection neurons. This means that the majority of the available maps are those received at the input to, or those created at the output of a signal processing engine. No mapping is currently possible of the complex mathematical manipulations being performed, in the analog domain, within the individual engines. Recently, an autoradiographic technique has appeared that provides a much more comprehensive map at a given location in the visual system.

There are multiple signal paths emanating from the retinas of the (typically in chordates) two eyes, and even more within the CNS. These signal paths can be described in terms of a number of intermediate points described as engines in this work. These engines may perform feature extraction or command generation functions. At the highest level, they can also be considered to perform abstract cognition. All of the engines receiving signals directly from the retinas can be considered to maintain retinotopic maps for one purpose or another. These maps can usually be probed in order to define their principle axes and degree of conformality relative to the initial retinal maps. However, it is usually found that the maps along the path leading to the posterior occipital lobe do not exhibit a spatial resolution comparable to that of the original map. On the other hand, each point probed on these intermediate maps exhibits a receptive field that is very large relative to the pixel size of the original retinal maps. The effect is similar to that expected if the retinal image was re-imaged onto the new map using optical techniques but failing to achieve focus. However, this is an incomplete analogy. The signals in the new map are related to the original map through complex mathematical relationships that are quite different from those of an optical projection. Eventually, the concatenation of these complex mathematical manipulations result in a totally abstract representation of the image projected on the retinas.

Robinson, et. al. have studied the receptive fields of probed neurons in the parietal lobe of rhesus monkeys in considerable detail. As shown in Robinson, et. al\textsuperscript{58}, the receptive fields of these neurons in response to even simple stimuli exhibit a large area of overlap because of the complexity of the stimuli normally employed in the laboratory and the amount of signal manipulation employed. Such large degrees of overlap make it extremely difficult to assign a specific role to a specific morphological area. In the case of Robinson, et. al., their stimulus was a 3° by 3° white square, a stimulus considerably larger than the foveola, and therefore, representing a “mixed stimulus” in terms of the signal processing and perceptual systems.

The power of the findings of Robinson, et. al. are so significant to establishing the context for addressing the literature of cortical function that it is presented in Figure 15.1.2-2 prior to any significant discussion of higher level

perception. Clearly, the use of a simple square “white” light stimulus leads to major confusion in interpreting data obtained employing electrophysiology or nuclear imaging at their current level of spatial resolution relative to the cortex.

Investigators have always attempted to associate various areas of the brain with a topographical representation of the retina. This procedure has always shown a cursory correspondence at best and has frequently encountered anomalies, such as the fact that the signals from the foveola are not normally found within the topographical map of the LGN and V1. In general, the concept of a topographical representation of the retina becomes more difficult to support as one moves to areas V2 and V3. Such mapping becomes controversial in V4 and essentially does not exist in areas anterior to V3 and V4. On the other hand, the areas of the cerebral cortex anterior to V3 and V4 are found to receive visual signals directly from the PGN/pulvinar couple rather than via the LGN and V1. They are also found to send signals to the superior colliculus that control both the optokinetic response and other skeletal responses of the animal to a threat. These differences suggest that there is a different system design and architecture involved in the topology of the cerebral cortex than usually assumed. It requires a careful determination of the functional requirements placed on the cerebral cortex before proceeding.

When the axes and degree of conformality of the intermediate maps are determined, relative to the original images on the retinas, it is frequently useful to describe the orientation of the intermediate map. Because of the curvature usually encountered, the orientation can be described in terms of a global or average angle between the map and the original image. Alternately, a local sign, or field sign, can be defined to describe the angle between points in the intermediate map (relative to the axes of that intermediate) and the points in the retinal map relative to its major meridians. This latter process is seldom done with precision because virtually all previous investigations have assumed a flat field for the focal plane of the optical system of the eye. The focal plane of the physiological optics, properly known as the Petzval surface, is nearly a sphere.

Sherman & Guillery have provided brief remarks concerning the use of the term “local sign” and the concept of diffuse signals (pg 12). Their concept of diffuse signals being arranged randomly within a map is as they say “a relationship that is not easy to demonstrate.” In this work, as the signals become less retinotopic and more abstract, the relationship between the signals and any graphical representation becomes vanishingly small.

Many investigators have found the global sign to be reversed between adjacent maps relative to their expectations. It is not normally clear from the literature what their expectation were based on. Did they expect the images to invert at alternate locations as in the case of simple optical imaging? Alternately, did they expect all of the images to maintain a similar organization like frames in a comic strip? A casual analysis would suggest that the conformality of the typical map is controlled by the amount of signal processing power required, on an area to accomplish the task. Both the global and field signs between adjacent maps are more likely determined by the desire to minimize the signal projection distances between related areas than any other consideration.

For precise work, it is proposed that the concepts of local sign and local magnification factor be subjugated to the
more fundamental concept of a field map. If regularly spaced horizontal and vertical lines are introduced into an image in object space (or the retinal image if appropriate), their representation in a projection at the location of interest will provide a mesh of local unit vectors (a common practice in electromagnetics). These vectors describe the local magnification factor, angle of the field vector relative to the edges of the field and the relative curvature of the field lines. This type of projection is now available for the striate cortex of the Macaque monkey, see Section 17.2.3.

It is useful to have a table describing the location, scope, conformality, and relative abstractness/retinotopy of various major maps known to exist in the human visual system. Beyond the optical chiasm associated with the optic nerves, there are two distinct signal processing paths that process the data from the foveola and the peripheral retina separately. The abstract signals generated from the engines along these paths (grouped into couples here) are both passed to the thalamic reticular nucleus for projection along the same path to the parietal and anterior lobes of the cerebral hemispheres. As will be described later in detail, the map projected to area 17 of the occipital lobe does not contain an area mapping the foveola. The foveola is mapped via the PGN/pulvinar couple. This allows a table of maps to be divided into three distinct groups, those associated with the LGN/occipital couple, those associated with the PGN/pulvinar couple, and those associated with the parietal and anterior lobes. **TABLE 15.1.2-1** provides one summary of these maps for reference when discussing this chapter. It will not be justified or even explained at this time. However, its relevance will become clearer as the operation of the visual system is explored in the main body of the chapter. It is consistent with the architecture of vision ca. 2002 as presented in **Section 15.6.4.**

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<table>
<thead>
<tr>
<th>LOCATION</th>
<th>SCOPE</th>
<th>CONFORMALITY</th>
<th>RETINOTOPICITY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Object space image Retinas</td>
<td>Unlimited</td>
<td>Locally high</td>
<td>Variable</td>
</tr>
<tr>
<td></td>
<td>Full monocular field</td>
<td>Reference</td>
<td>Perfect</td>
</tr>
<tr>
<td>PGN/PULVINAR PATH</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PGN/pulvinar couple</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>input</td>
<td>Binocular achromatic</td>
<td>High</td>
<td>High (foveola only)</td>
</tr>
<tr>
<td>output to TRN</td>
<td>Merged achromatic</td>
<td>Vector</td>
<td>Abstract</td>
</tr>
<tr>
<td>output to POS</td>
<td>Servo signals</td>
<td>Vector</td>
<td>Abstract (fine pointing &amp; scanning)</td>
</tr>
<tr>
<td>LGN/OCCIPITAL PATH (geniculocalcerine path)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LGN/Occipital couple</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>input to LGN (to left &amp; right)</td>
<td>two monocular</td>
<td>Spherical/spatial &amp; time dispersed</td>
<td>High (periphery only)</td>
</tr>
<tr>
<td>(lum &amp; chrom.)</td>
<td>aligned monocular</td>
<td>Spherical</td>
<td>High</td>
</tr>
<tr>
<td>internal to LGN</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(lum &amp; chrom.)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>output to POS</td>
<td>Servo signal</td>
<td>Vector</td>
<td>Medium (crude pointing)</td>
</tr>
<tr>
<td>output to Occip.</td>
<td>Spatially merged</td>
<td>Spatially distorted/ time dispersed</td>
<td>High (periphery only)</td>
</tr>
<tr>
<td>(lum &amp; chrom)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>input to Occip.</td>
<td>Spatially merged</td>
<td>Spatially distorted (lum &amp; chrom aligned)</td>
<td>Medium (periphery only)</td>
</tr>
<tr>
<td>(lum &amp; chrom)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>output of Occip.</td>
<td>Abstract features</td>
<td>Vector</td>
<td>Abstract</td>
</tr>
<tr>
<td>(returned to TRN)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PULVINAR/PARIETAL PATH (pulvinar pathway)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PGN/pulvinar signals to TRN</td>
<td>Abstract foveola features</td>
<td>Vector</td>
<td>Abstract</td>
</tr>
<tr>
<td>LGN/Occipital signals to TRN</td>
<td>Abstract peripheral features</td>
<td>Vector</td>
<td>Abstract</td>
</tr>
<tr>
<td>TRN to parietal/anterior</td>
<td>All abstract features</td>
<td>Vector</td>
<td>Abstract</td>
</tr>
<tr>
<td>(saliency format)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TRN to superior collic.</td>
<td>Abstract commands</td>
<td>Vector</td>
<td>Abstract (but interpretable by SC)</td>
</tr>
</tbody>
</table>
Investigators have occasionally attempted to define a magnification factor between two “maps” associated with the visual system, probably most frequently between the retina and the LGN. Because of the lack of the lack of orthogonality and the lack of conformality, both globally and locally in the various maps, it is difficult to define a magnification factor of general utility. The difficulty of defining such a magnification factor for the visual cortex can be seen from the maps presented in [Section 15.2.5.5]. At best, a magnification factor related to a given map should be given as a complicated function of retinal location. This function can then be integrated along certain axes or within specific local regions to give a specific value under those spatial conditions.

Many investigators have studied the retinotopic maps of other species. Sanderson has presented interesting material relating failures in retinotopicity that can be correlated with albinism in a variety of species\textsuperscript{60}.

15.1.2.3.5 Problems in determining the biochemistry of the neural and cognitive processes

Investigators have struggled for many decades to explain the processes of cognition and memory based on strictly chemical mechanisms. Little progress has been achieved. In 1981, Rose summarized the problem by raising two questions\textsuperscript{61}. What do we think we are looking for? How will we known when we have found it? He went on to hint at the possibility that the causal or correlative relationship between the biochemical state and behavioral expression was inadequate. He went on to identify the task of neurobiology as identifying the necessary, sufficient, and exclusive biological correspondence of the processes used in the central nervous system and memory formation through a set of criteria. He defined an engram as the description of a putative process that met this criteria.

In this work, the fundamental neuron and its operation have been described in detail based on electrolytic mechanisms and processes. It has not been necessary to invoke chemistry except in order to provide the power necessary to operate the electrolytic devices, the Activas.

When it comes to cognition and memory, the neural system shows many similarities to modern computers and memory modules. This chapter will proceed to describe the operation of the central nervous system in strictly electrolytic terms. No operational requirement is placed on chemistry with regard to the performance of the neural system, except to provide electrosthenolytic power and the growth of new synapses as required.

15.1.2.3.6 Problem with anesthesia in higher level perception

In the field of brain research related to vision, it is common to anesthesize the animal, dilate the pupils and immobilize the muscles of the eyes. As will be shown in this chapter, the immobilization of the eye muscles pharmacologically has a severe impact on the operation of the visual system, particularly with respect to higher level perception by the brain. In the absence of normal tremor of the eye, the Precision Optical System of the eye is ineffective. The signals related to the foveola, that are extracted by the POS, are not projected to the cortex! This has a profound impact on any research concerning the operation of the brain in response to signals from the foveola.

15.1.2.3.7 Problems in defining GABAergic and cholinergic mechanisms

\textsuperscript{60}Sanderson, K. (1975) Retinogeniculate projections in the rabbits of the albino allelomorphic series.\textit{J Comp Neurol} vol 159 pp 15-27
\textsuperscript{61}Rose, S. (1981) what should a biochemistry of learning and memory be about?\textit{Neurosci.} vol. 6, No. 5, pp 811-821
It is particularly difficult to follow the literature with respect to the effects of the glutamates (GABA, glutamate, aspartate and various intermediate products), and the cholines on the operation of the neural system. Similarly, the impact of a variety of pharmaceuticals is also variable. The impact of these materials is highly dependent on the method of application and the state of the specimen before application.

The basic premise that these materials are chemical neurotransmitters is not supported in this work. The actual mode of signaling between neurons was shown to be electrolytic (involving the transfer of electrons through a crystal of hydronium) in Chapters 8, 9, & 10 and specifically Section 8.7.4. This is not to say the above types of materials cannot irritate or otherwise impact the performance of a neuron. This impact is the subject of this section.

The basic mechanism of neurology involving the glutamates is shown in Eq. 15.1.2-1

\[
\begin{align*}
\text{Glucose} & \rightarrow \text{Pyruvate} \rightarrow \text{Citrate} \rightarrow \alpha\text{-Oxoglutarate} \rightarrow \text{Glutamate (4-5\%)} \\
\text{Alnine (1\%)} & \rightarrow \text{Oxaloacetate} \rightarrow \text{Succinate} \rightarrow \gamma\text{-Aminobutyrate (1-5-3\%)} \\
\text{Aspartate (2\%)} & \rightarrow \text{Lactate}
\end{align*}
\]

Glucose to GABA conversion in situ.  

This equation is key to understanding the in-situ operation of the neural system. It shows the operations and concentrations of the major energy source in the brain related to neural operations. A similar equation can be written for the other neurons of the body. The key part of the equation is the reaction of glutamate into GABA. This is the source of power to the neural system. It occurs as part of an electrostenolytic process that generates free electrons within the various plasma conduits of the neuron. These are typically the dendroplasm, the podaplasm and the axoplasm. In the case of long axons, additional axoplasmic conduits may be present. These are generally labeled axon segments or interaxons.

In other cases, the reaction converting glutamate into GABA is associated with a parallel NAD-NADP reaction that provides chemical energy to the tissue for metabolism growth and other purposes. This is an entirely separate reaction that may occur at or on a substrate. However, it does not involve an electrostenolytic reaction.

As shown each neuron typically has three separate sources of electrical power associated with it. Each dendritic, poditic and axonal plasma is supported by a separate electrostenolytic source of power. And, each of these sources of power depend on the conversion of glutamate to GABA according to the above equation. Of equal importance, the normal operation of these cells occurs when the bulk concentration of glutamate is about 4-5% and the bulk concentration of GABA is about 1.5-3%. The empirical difficulties arise when these concentrations are changed or the conductance of the interneural matrix supporting these neurons changes. Changes in this conductance may be
due to changes in the matrix or the presence of other agents that interfere with the transport of glutamate and GABA.

Two situations must be considered. First, the in-vitro experimentation with a single neuron. Second, the in-vivo experimentation related to a large number of neurons in a matrix.

It is common for experimentors to wash a single neuron before placing it into an in-vitro test fixture. This clearly disturbs the concentrations of glutamate and GABA found along the length of the neuron, and particularly at its electrostenolytic sites. As demonstrated in Chapter 8, stimulation of the dendritic terminal of a neuron, with an electrical voltage, causes an output voltage change in phase with the stimulation. On the other hand, stimulation of the poditic terminal causes a voltage response of opposite phase. Similar changes can be induced by changing the availability of the electrostenolytic reaction components required to generate the negative potential found within the various plasmas. This polarity difference is the fundamental source of most of the confusion in the literature. Assuming glutamate is present at the electrostenolytic site of the axon, the voltage potential of the axoplasm will be controlled by the potential difference between the dendritic and poditic terminals of the Activa within the neuron. This potential is dependent on the concentration of glutamate (and GABA) at the two electrostenolytic sites supporting the dendrites and the podites. The change in axoplasm potential as a function of the insertion of electrons into either the dendroplasm or podaplasm is of interest. If more electrons are injected into the dendroplasm, the potential of the axoplasm will become more negative (within its normal operating range). If more electrons are injected into the podaplasm, the axoplasm potential will become more positive. Thus, the net potential of the axoplasm is dependent on the concentrations, of glutamate (and GABA), available at the individual electrostenolytic sites. Whether the neuron reacts GABAergic or exhibits the opposite reaction (generally labeled cholinergic) depends on the location and concentration of the topically applied reaction components. Similarly, if other pharmaceuticals are introduced that change the the concentration of the electrostenolytic reactants or interfere with the normal conductance of the reactants to and from the sites, the axoplasm potential will be impacted.

Extending the above situation to the in-vivo case is straightforward. If the concentration of the glutamate or GABA, as reactants, is interfered with or their access to the electrolytic sites is interfered with, the response observed either electrophysiologically or psychophysically will change. Whether this change is positive or negative depends entirely on how the concentrations and conductances are changed at the various dendritic and poditic electrostenolytic sites. If the measured response is the result of the changes affecting many neurons in a complex series-parallel arrangement, as found in all neural engines, the change in output is largely probabilistic. This probabilistic outcome is the source of much of the confusion in the literature concerning GABAergic and cholinergic events.

At the fundamental level, GABA, choline and other pharmaceuticals can cause either a positive or negative outcome depending on the method of application of the material to the specimen under evaluation. Typically, in-vivo application of these materials causes a consistent effect because the relevant conditions are changed in a predictable way. However, this is not always true.

Based on gross application of the above materials in-vivo, an material is considered GABAergic (GABAergic like) if it causes the same change in output as the application of GABA would. A material that impacts the specimen in the same manner as the application of AcetoCholine does is considered cholinergic. At a more refined level, the reactions of various materials have been classified into more (largely empirical) categories. See Affi & Bergman for a short discussion of these categories.

15.1.2.4 Use of experimental animals and reporting traumatic conditions

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It is a difficult problem in surgery and instrumentation to obtain uniquely specific information concerning specific signal paths and signal processing in the neural system. Much of the available information is obtained from humans following traumatic accidents. With that source extremely limited, surgically modified animals have frequently been used to emulate the desired condition as closely as possible. To this end, Noback provided a framework for discussing these two classes of modified neural systems in 1967.63

1. The “spinal animal,” i.e., one with its spinal cord transected,

2. the decerbrate animal, with its brain stem transected at a low midbrain (mesencephalon) level,

3. the “midbrain animal,” with its brain stem transected at a high midbrain level,

4. the “thalamic animal,” with its cerebrum transected at a “high” thalamic level, and

5. the decorticate animal, with its cerebral cortex ablated.

Forty years have passed. For purposes of this work, it is important to make these terms more specific, and to be sure they are compatible with the definitions of Section 11.1.4 and Section 2.3.1. Figure 15.1.2-3 shows Figure 2.3.1-1 modified to show the defined transection points and an additional series of points. The location of the transections are defined based on the written descriptions of the animals behavior following surgery provided by Noback.

It is important to mention that a simple hierarchal diagram like this does not show the importance of the thalamic reticular nucleus to the overall operation of the neural system. Transection number 4 is shown as isolating only the data processing portions of the thalamus. It does not transect the supervision and control portions of the TRN. It only isolates the portion of the TRN comprising the associative memories consisting of the LGN, PGN and the MGN (associated with hearing). Nearly all of the signals passing to and from the telencephalon also pass through the TRN operating in its supervisory (and probably switching) function. If the supervisory portion of the TRN is isolated from the brainstem, the effect is similar to performing a transection at location 2.

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The added points provide two additional categories of transections, those relating to the optic nerve and those related to the cerebral cortex. The complexity of the interconnections between the two two retinas and the brain via the optic nerves is a source of considerable information concerning the organization of the visual system. Section xxx has addressed the impact of transecting the optic nerve under a variety of conditions (transections A through H). It is also useful to examine the decorticate animal more precisely by specifying what lobes have been ablated or otherwise isolated from the remainder of the system. (transections T through Z). A simple tree structure is not adequate for describing this case since the brain is not a hierarchal structure. Within the brain, the individual lobes operate in a more complex interconnection arrangement, in conjunction with the control and switching capabilities of the thalamus. This bidirectional communications between the individual lobes and the thalamus has demonstrated the limited importance of direct connections between the lobes (with the exception of the frontal and parietal lobes). Transections between the other lobes have been shown to have minimal impact on the performance of both test animals and, in a few instances, humans. Another transection not easily shown in the above hierarchal tree is the transection of all major commissure between the two halves of the cerebral cortex. Such transections (described as xxx) have shown to have minimal impact on the visual system in humans. The merging of the data from the left and
right visual fields is unaffected and stereographic vision remains normal.

15.1.3 The theory and operation of the fMRI technique

Functional magnetic resonance imaging, a form of nuclear magnetic resonance imaging, is rapidly taking an important place in interpreting the operations of the brain. Although of relatively low spatial resolution (the term voxel is used to describe the three-dimensional resolution of the technique) and slow, the results of the technique are easily interpreted. Voxels as small as 1 mm³ are currently achievable. A complete brain can be scanned at this resolution in about six minutes. Smaller voxel sizes can be achieved over volumes smaller than the human brain. However, problems of internal heating are beginning to limit the potential of the technique. Buxton has recently provided a major text on the technique, its past results and future potential⁶⁴. Young has edited a major volume on medical imaging⁶⁵. He has provided a large glossary, list of acronyms and list of abbreviations. Edelman, et. al. have also edited a large clinical volume on MRI⁶⁶. Chapter 8 in Edelman, et. al. and Buxton are the most useful at the research level.

The fMRI technique is based on the measurement of the magnetic spin of certain nuclei present in the body. The field is very active at this time exploring alternate materials and methods of selecting materials containing effective nuclei. Diamagnetic and paramagnetic materials may be used. The paramagnetic properties of oxygen are particularly convenient in the BOLD technique. BOLD stands for Blood Oxygen Level Dependent effect. While not necessarily the most sensitive, it is obviously convenient and understandable. Oxygen plays a crucial role in the overall metabolism of the brain. However, tests more tailored to neural activity (as separate from overall metabolism) would clearly be more useful.

Buxton describes in detail a conundrum faced by the imaging community at this time. While the original technique was based on the assumption that the local oxygen level within the brain would decrease during significant mental activity, the opposite has been found to be true. Buxton describes several alternate theories designed to explain this paradox. However, this work provides an additional alternate theory.

Being a non-intrusive technique, the theory of fMRI relies upon a variety of poorly calibrated phenomena, and the ratios between these phenomena. The initial theory was based on the premise that the rate of glucose consumption and the rate of oxygen use would rise proportionately during mental activity. This theory was based on the assumption that the metabolic activity increased. The theory revolves around the cerebral blood flow (CBF), the cerebral metabolic rate of glucose (CMRGlc) utilization and the cerebral metabolic rate of oxygen (CMRO₂) utilization.

A key finding is that of Marchal, et. al²⁷. Studies of resting distribution of CMRO₂ in the brain have found a rather uniform O₂ extraction fraction of about 40% from the blood circulating within the brain. Under these conditions, the ratio of oxygen consumption to glucose consumption is about 5:1., which approaches the ratio for the complete oxidative metabolism of glucose (6:1). This data suggests a simple, and expected, coupling between the CBF and metabolism at rest. A similar coupling has been shown to exist between the CBF and the CMRGlc under both resting and active conditions.

The striking finding was that the CMRGlc increased in proportion to the CBF, but the CMRO$_2$ did not. Fox & Raichle found that a 29% increase in the CBF was accompanied by a similar increase in the CMRGlc but only a 5% increase in the CMRO$_2$. The result was that the relative concentration of oxygen at the site of mental activity actually went up. New theories had to be assembled quickly to account for this situation.

The fMRI technique is a Blood Oxygen Level Dependent (BOLD) technique. It relies upon the change in oxygen concentration in the local supply in a very complex manner. The concentration depends on both the blood flow rate and the rate of change in the constituents of the blood containing oxygen. A major indicator is the signature of the paramagnetic material, deoxyhemoglobin (dHb). Here is where the operation becomes murky. The common position is that if the nominal local CBF increases by 30% and the oxygen metabolism only increases by 5%, the O$_2$ extraction fraction must drop to about 32% net (from 40%). As Buxton says, “Although the underlying reasons are still unclear, it appears that a strong imbalance in blood flow and O$_2$ metabolism is a common occurrence during brain activation.” He also notes, “The large imbalance in the changes in CBF and CMRO$_2$ was described as an uncoupling of flow and oxygen metabolism during activation, in the sense that the large change in CBF seemed to serve some need other than increased oxygen metabolism.”

Buxton addresses a variety of the current theories for the low extraction of oxygen from the local blood supply of the brain during mental activity on his pages 44-57. One theory accounting for the mismatch is the oxygen limitation model (Buxton & Frank, 1997). This model suggests that there is a barrier between the capillary bed and the brain tissue that limits the transfer of oxygen and that the flow through the bed is increased to overcome this difficulty. Buxton concludes with a caricature of the problem. This figure is modified substantially in Figure 15.1.3-1 below.

### 15.1.3.1 Theory of fMRI based on this work

This work suggests an alternate theory for the operation of the fMRI technique. It is based on the differentiation of cell metabolism into two distinct components. The first component relates to the energy consumption of neurons related to signaling. The second component relates to the other metabolic function found in all cells of the organism. This second component is the component discussed in the current literature associated with fMRI. The first component is distinctly different. It is the component associated with the electrostenolytic process providing electrical power to the neurons of the organism. This power is derived from the conversion of glutamate into $\gamma$-aminobutyric acid (GABA) on specialized regions of the surface of the neurons.

The operation of the power supply to the neurons is discussed in detail in Section 8.6. The provision of electrical power to the neurons involves an electrostenolytic process on the surface of the individual neurons. This process consumes glutamic acid. Glutamic acid is produced from glucose by various paths around the citric cycle. The key factors are that glutamic acid (glutamate) can not cross the blood-brain-barrier to enter the brain. Therefore, it must be manufactured in-situ within the brain. Thus, the glucose consumption of the brain must contain portions supporting the production of glutamic acid and the other metabolic processes of the brain.

The consumption of oxygen within the brain is determined by measuring the presence of oxygen within the deoxyhemoglobin molecule (dHb) which is paramagnetic.
15.1.4 Glossary

**Afferent**—Carrying inward to a central organ or section, as nerves that conduct impulses from the periphery of the body to the brain or spinal cord. See also efferent.

**Bifurcation**—A dividing of a structure. When used to describe a signaling channel, it supports two separate interpretations. The subchannels within the structure may *branch* in order to go to two distinct terminals simultaneously, or some subchannels may *be routed* differently than others in order to serve individual destinations. Each optic nerve bifurcates twice in the process of terminating in the brain.

**Blind sight**—Sight wherein all of the sensory functions of the visual system are operating normally but one or more of the feature extraction engines and/or the associated recognition functions have failed. This condition can be congenital, due to disease, or due to an accident. Stroke frequently leads to this type of problem.

**Command**—A neural message executable by the PNS (including the oculomotor subsystem) and generally originating in the superior colliculus and associated structures. Usually using a bit-serial word format and transmitted over a single (or redundant) neuron. See Instruction.

**Comparator**—A nominally analog differencing circuit, that may be operated in synchrony with a clock or asynchronously, incorporating sufficient gain to force the output signal into saturation. Such circuits are typically used to provide one or more of three indications, $X>Y$, $X<Y$ or $X=Y$. By using multiple individual comparators in logic circuits, significant characterization of a large group of input signals can be provided.

**Cholinergic**—An action that is excitatory with respect to the output of a neuron. See main glossary.

**Diamagnetism**—A magnetic property of an atom arising from the affect of all of its electrons attempting to align themselves with an applied magnetic field.

**Diencephalon**—Sometimes described as the fore brain (not to be confused with the anterior lobe of the cerebrum). The most prominent portion of the diencephalon is the thalamus. However, the fornix, amygdala and the thalamic reticular nucleus are also of great importance.

**Efferent**—Directed away from a central organ or section. Carrying impulses from the central nervous system to an effector. See also afferent.

**Enzyme**—An organic catalyst; providing a variety of functions and frequently defined in terms of its internal groups and/or the material it catalyzes. The internal groups are frequently a protein element (the apoenzyme) and a non-protein group (the prosthetic portion). Many enzymes require a cofactor or coenzyme to act as acceptors or donors of a functional group that are added or removed from the substrate.
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Hydrolitic enzymes—addition or removal of the elements of water
Hydrase—addition or removal of water
Isomerase—catalyze an intramolecular rearrangement
Microsomes—microsomes (particulate bodies) within cells act as (are) enzymes
Phosphorylases—
Oxidation-reduction enzymes
  Dehydrogenase—
  Oxidase—
  Monoxygenase
Transferring enzymes—transferring amide, amino, methyl and other groups
  Transmethylation
  Transoxygenation
Transporting enzymes (Binding Proteins)

Field sign—A characteristic associated with a map that is projected faithfully relative to the antidromic signals. In precision work, the field sign will be at different angles for individual small areas of the overall map. As the information becomes more abstract, the concept of a field sign fails.

GABAergic—An action that is inhibitory with respect to the output of a neuron. See main glossary

Instruction—A neural message not executable as a command by the PNS. Used to direct the actions of the superior colliculus and thalamic reticular nucleus. Typically found in the alarm mode, volition mode and other channels within the CNS. Usually encoded as a bit-parallel word and transmitted over a group of parallel neural paths. See Command.

Lateral Geniculate nuclei—Structures at the posterior of the thalamus receiving and processing the majority of the neurons associated with the non-foveola portion of the retina before passing the resultant signals to area 17 of the occipital lobe of the cortex and also to the pulvinar area of the thalamus. See Brodal, 1981, and Pretectum below.

Local sign—See field sign.

Machine language—The basic system of symbols used to create the vectors, consisting of both the instructions that control and transfer information within any computational device and the format of that information.

Macular sparing—A condition encountered in situations where V1 is essentially destroyed but the subject can still read and fixate on objects.

Metabolism—The molecular level events involved in the synthesis, assembly, maintenance, and turnover of cells, groups of cells and components of cells in an animal. The function includes the provision of power to the neural system but not the processing and transmission of signals.

Neglect—A medical condition where the subject entirely ignores the side of his body and the side of his visual field sensed by a damaged portion of his brain, generally associated with damage to the cortex. Usually a result of a stroke in the elderly. May be due to physical damage or disease.

Neural network—1. Neurology, A description of the topology of an engine within the CNS most easily interpreted as a Boolean network of fundamentally linear circuit elements. When overdriven, these fundamental circuit elements can provide AND, OR, NOT AND (NAND), NOT OR (NOR) and other simple logic functions.
The circuits are basically self-clocking and asynchronous with respect to individual input signals. The output signals are fundamentally analog and continuous (not obviously clocked).

**Ontogeny**—The total of the stages of an organism's life history.

**Paramagnetism**—A magnetic property arising from the affect of unpaired electrons aligning themselves with an applied magnetic field.

**Pretectum**—A term used variously by investigators and depending on the phylogeny of the specimen. It is frequently defined as the rostral portion of the tectum. Alternately, it is associated with the posterior portion of the thalamus where it can be synonymous with the ventral tier thalamic nuclei of other authors. In both cases, neurons from the retina terminate at this location. In humans, the pretectum generally includes the pulvinar, and multiple ventral areas of the thalamus but does not include the lateral geniculate nuclei. See Brodal (1981), Leventhal (1991) and Lateral Geniculate Nuclei above. Additional discussion appears in Section 15.6.

**Purkinje cell**—The only morphologically recognized type of output neuron of the cerebral cortex.

**Receptive field**—The angular field in object space to which a given neuron at some point within the visual system responds, in any way but usually determined based on the occurrence of action potentials of ganglion cells.

**Riddoch Syndrome**—See Blind sight.

**Saliency engine**—A higher level mechanism in perception that provides the addresses of pieces of perceived information that must be considered as a group to achieve cognition. The various vectors (engrams), relating to the perceived information, when grouped act as individual bytes in the overall cognition vector describing the recognized event.

**Saliency spreadsheet**—A putative collection of high level cognition vectors (or series of addresses to lower level perception vectors) that constitute the basis of cognition.

**Stereopsis**—The process of merging the two images, acquired by the eyes from different points in space, into a useful image by eliminating the parallax and obtaining distance cues. See Hubel (1988).

**Substrate**—Used variously.

1. Biology, the molecule on which an enzyme exerts catalytic action.
2. Surface chemistry, the surface upon which reactants accumulate and react.

**Thalamus**—The inner chamber. Part of a very complex area between the top of the spinal cord and the proliferation of the cerebral cortex. Easily looked upon as a mere switching point but clearly performing significant signal manipulation within its numerous individual engines.

**Traffic analysis**—A term used in military intelligence and applicable to uncovering the interconnections found within the neural system. Generally, the observation of signals emanating from or arriving at a given location and relating them to other terminal locations.

**Tremor**—The fine angular vibration of the eye used to provide relative motion between the scene and the eye, thereby allowing the change detectors of the eye to create signals used by the brain to perceive an image. The amplitude of the tremor is the most important parameter. It is reported to be 20-40 arc seconds in Man (corresponding to one or two photoreceptor diameters in the fovea). The frequency in Man is difficult to measure, the data ranges from 30-90 Hertz with reports to 150 Hertz.
Zombie – a subject capable of acting just as normal people do but to be completely unconscious.

15.1.5 Terminology & Coordinates

The Committee on Colorimetry in the Science of Color took pains to define the difference between perception and sensation. It defined sensation as the “mode of mental functioning that is directly associated with stimulation of the organism”. It defined perception as the “mode of mental functioning that includes the combination of different sensations and the utilization of past experience in recognizing the objects and facts from which the present stimulation arises”. Helmholtz hypothesized that the colors we see are perceptions that involve a number of different sensations. This Chapter clearly involves these concepts of perception; it is very much involved with the synthesis of multiple signals into a comprehensive and comprehensible whole, whether it be a scene, a message or a cue. However, another degree of freedom is needed in the above concepts. Continuing the approach used so far, sensation involves signals prior to any analyses and cognition includes signals involving analyses. Cognition includes the initial analyses, or perception, followed by cognitive analyses, or recognition. The distinction between perception and recognition is important because at least a fundamental part of perception is performed without the knowledge of the animal. It is the recognition of the signals delivered to the higher centers, by both the visual and other systems that results in awareness of the situation by the animal. This awareness supports further willful response.

15.1.5.1 Perceptual field of view

There is a common desire to treat the eye as the analog of a camera. This leads to the further analogy of the retina as a piece of film and the field of view of the retina as encompassing the total perspective of the brain with regard to visual information. These analogies need to be discussed in greater detail. As discussed in the Chapter introduction, the information from the eye needs to be placed in a larger context that is compatible with the information received from other sensory inputs. Rodieck uses this subject as a theme for his recent book68. As also discussed in the Introductory Chapter (one of the reality checks), it is clear that the perceptual field of view utilized by the brain is much larger than the instantaneous field of view of the eye, or the pair of eyes. For humans, this total perceptual field of view is on the order of 180 degrees wide in the horizontal plane and approximately 150 degrees in the vertical plane of the head. This perceptual visual field is essentially fixed and oriented relative to the body of the animal. The instantaneous visual field of each eye is considerably smaller than, and spatially independent of, this overall perceptual visual field. Therefore, if one thinks of the overall perceptual field of the brain as a very large “spread sheet”, the data received from each sensor, visual or otherwise, must be placed at the appropriate position in this spread sheet. If the spread sheet is thought of as multidimensional, it is easy to conceive of one layer of the sheet for audio input, one for mechanoreceptor inputs, one for chemicoreceptor inputs and one or more for visual inputs (since color, form, stereoptic properties, etc. may be entered separately after having been determined during previous processing).

It is important to point out that the above spreadsheet does not represent a literal mapping of the spatial inputs from the visual system. It is a map of abstract vectors, or engrams. These vectors exhibit only a cursory relationship to actual luminance values. See Section 15.2.2 below.

The manner in which visual information is inserted into the spreadsheet is similar to that portrayed in many ancient paintings (where a beam of light appears to emanate from the eye) and similar to the current situation of a person walking in the dark with a flashlight. The brain maintains an overall perceptual field in memory which is updated on a zone basis with data obtained from within the visual field of the flashlight (eye).

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Although not critical to this work, it is interesting to explore the neuro-motor signals transmitted by the brain for purposes of pointing the eye, and contemplating how the brain places the returned visual data in the spreadsheet. It is well documented that the eye is driven by the muscle system in response to signals from the brain in an open loop manner from a servomechanism point of view. That is, the brain has learned over a period of time the mechanico-dynamic properties of the eye. It therefore generates drive signals for use by the muscles without expecting any signals in return indicating whether the eye actually turned to the specified direction. The eye then places the returned visual information in the spreadsheet at the location that it anticipated the eye was turned to by the muscles. If the eye does not turn to the desired direction, or the platform on which the eye is mounted (through the body) changes orientation in an unexpected manner, the brain places the new information into the spreadsheet at a location that is inappropriate and the tertiary and higher processing levels in the brain immediately signal a problem that we know as various forms of vertigo.

As will be discussed further below, in the absence of motion between objects in the object plane and the line of fixation of the eye, little or no data is generated by the retina and the animal is essentially blind. Both Yarbus and Ditchburn discuss this reality in considerable detail, even to whether the perceived image should be described as black or “null”. Based on the model developed here, and the fact that the eye does not maintain any absolute brightness level, it appears that “null” is the more appropriate term.

15.1.5.2 Perceptual Coordinate System

Based on the above discussion, it is important to define a set of coordinates that are appropriate to the overall perceptual field of the animal as well as the necessary local coordinate systems. It appears that the overall coordinate system for the case of humans is most logically described by a polar system consisting of a horizontal plane, probably containing the geometric centroid of the two eyes (modified slightly by the known lateral motion of the eyes when rotating) and a vertical plane passing through the nose and perpendicular to a line passing through the centroid of the two eyes. Using this set of coordinates, the primary fixation point for the overall visual field is \( \rho = 0, \theta = 0 \) with \( \rho \) taken as the elevation angle, a position directly in front of the individual’s head at eye level. Hering used a series of terms that can be placed in this context. He spoke of absolute visual directions as being stable despite eye movements and change in fixation point. These absolute directions match the overall coordinate system defined here. Hering also spoke of subjective visual directions as relative to the principle visual direction of an eye. This principle visual direction was defined as a line between the fovea and the center of the iris at a given instant. Since the fovea is not located on the optical axis of the eye, the principle visual direction has a set of angular coordinates that are not \( 0,0 \). Because of this, the angular coordinates of an object point expressed in overall visual field angles is obtained as follows:

- the subjective field angles relative to the fixation point
- plus the offset angles associated with the fixation point relative to the geometrical axis of the eye
- plus the pointing direction angles commanded by the brain
- equals the overall perceptual visual field position angles.

It is immediately seen that the set of overall perceptual field angles may be well outside of the instantaneous field established by the maximum subjective field angles of a given eye. In this case, the brain relies on past images that are stored in memory.

15.1.5.2.1 Contralateral versus ipsilateral in vision

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The terms contralateral and ipsilateral arose in discussions related to the somatosensory surface of the body versus locations stimulated within the brain. However, it has come into conflicting use when discussing vision. The term contralateral generally means situated on, pertaining to or affecting the opposite side of the body. Ipsilateral generally means situated on, pertaining to or affecting the same side of the body. However, the operation of the visual system is more complex. The neurons from each eye are sorted at the optic chiasm. In general, the signals from the left half of object space proceed to one side of the brain and the signals from the right half of object space go to the other. The signals are also separated by superior and inferior groups relative the the horizontal meridian. However, there is another group of neurons related to the foveola that are separated and treated differently. The general situation is illustrated in Sections 2.2 & 2.3. The more detailed situation is shown in Section 2.8.

15.1.5.3 Parallax

Ogle in the previous reference discusses several inconsistencies in geometric perception related to the visual process without introducing the subject of parallax. Since neither eye is at the center of the coordinate system defined above, careful work requires the recognition of these offset positions. The brain is aware of this offset condition and sends slightly different commands to the muscles of each eye in an attempt to reduce the data processing load required after the data is received at the brain. This can best be appreciated by expanding the above brief calculation into separate columns for each eye. The brain is also aware of the approximate distance to the object of interest from earlier data processing and sends any necessary commands to the muscles controlling the lens to adjust the depth of focus of the system. The brain then processes the data returned by the two eyes taking advantage of the difference in the two sets of signals to obtain stereoscopic information when feasible. However, when the brain processes the data of particular interest to obtain stereoptical data, some data from different depths of visual field from that related to the subject of interest is processed incorrectly and may generate clearly unrealistic perceptions. This involves the subject of parallax. This author believes the language used by Ogle is imprecise and fails to separate the concepts of principal visual directions of the individual eyes from the primary fixation point for the overall visual field. With this clarification, the quoted “Law of identical visual directions”, which was not stated specifically by Ogle, becomes immaterial.

15.1.5.4 The Blink Reflex

Referring again to Figure 1.5.2-2, it should be pretty clear that since the eye receives and processes visual information continuously as long as the eye lid is retracted; a serious problem can occur if information is obtained while the eye is in rapid transient motion on the way to another pointing angle. To avoid this problem, the eyelid is commanded closed during the interval of eye rotation, i.e., during the interval calculated by the brain for the eye to rotate to a new pointing angle. With the eyelid closed, little signal information is applied to the photoreceptors and no significant amount of information is transmitted by the eye to the brain. When the eyelid reopens, the brain processes the received information into the spreadsheet based on the pointing angles it commanded earlier.

15.1.5.5 Energy vs. Flux based laboratory testing

It is important to develop the difference between testing using equal energy spectrographic testing and equal photon flux based spectrographic testing. In the past, it has been normal to perform vision testing based on equal energy per unit wavelength sources. This has been considered standard for a number of reasons:

+ It is relatively easy to obtain a light source that exhibits an equal energy per unit wavelength characteristic, either a 7053 K light source or a incandescent lamp at 2870 K and a suitable filter. Unfortunately, the use of a
filter with a 2870 K source requires a very high intensity source. It may also require what is known as a cold filter (reflective in the infrared) to reject the heat from the source and avoid damaging the filter.

+ Most thermal detectors and even radio circuits that are thermal noise background limited are appropriately tested using equal energy per unit bandwidth sources.

+ Most engineering applications of color photometry have been developed based on incandescent light sources of a specified thermal temperature.

However, recent tests have demonstrated that the animal vision system utilizes a flux detector (photons), similar to a photo multiplier tube or solid state silicon photodetector, and not a thermal detector like a bolometer. Based on this fact, it is appropriate to calculate the quantum efficiency of the visual system based on the efficiency of the visual system at detecting photons. If the spectral performance of the system is plotted as a function of wavelength, a line of constant efficiency is a horizontal line only if the input test signal contains equal number of photons per unit wavelength. The energy of a photon is inversely proportional to its wavelength. Therefore, an equal energy per unit wavelength test signal contains a variable number of photons per unit bandwidth and lines of constant quantum efficiency on a spectral plot based on an equal energy per unit wavelength light source consist of a family of hyperbolic curves. Rodieck has recently addressed this subject.\(^1\)

The most important consideration related to the above paragraph is that the peaks, minimums, and inflection points of a spectrum should be taken with regard to a line of constant efficiency and not necessarily a horizontal line. The result is that the spectrum recorded using an equal energy light source will exhibit peak wavelengths relative to the horizontal axis that are displaced to the right (toward a longer wavelength) of the true peaks relative to lines of constant quantum efficiency; peaks relative to the horizontal axis may not be peaks at all relative to the lines of constant efficiency. Figure 15.1.5-1(a) and (b) illustrates this important difference. All spectral plots presented in support of vision research should be explicitly marked as to the nature of the light source used in their preparation. Theoretical sensitivity spectra as presented below are inherently equal flux per unit bandwidth based, i.e. the output per photon input at a given wavelength. They must be convolved into an equivalent equal energy spectra if they are to be compared in detail to response spectra acquired using an equal energy light source.

### 15.1.5.6 Signal recovery in an edge detector

The left frame of Figure 15.1.5-2 caricatures the foveola of the human eye illuminated by a single point source passed through the lenses of the eye. For purposes of discussion, only one type of photoreceptors is shown and the photoreceptors are assumed to be square. The illuminated spot is also assumed to be square. Note only the edges between the individual photoreceptors are shown. The solid line in the upper right frame shows the signal generated by the passage of the illuminated spot across the center photoreceptor. This signal will be labeled \( R_k \). The dashed line shows the signal generated by the passage of the spot across the next photoreceptor to the left in the foveola, \( R_{k-1} \). The middle-right frame shows the difference signal obtained, \( \Delta R \). The lower-right frame shows

\[ \text{Figure 15.1.5-1 Signal recovery in an edge detector. Left, an idealized view of the center of the foveola with a single point of illumination from the optical system. Idealized to show a square illuminating spot and only the edges of the photoreceptors (also assumed to be square for discussion). Note the importance of the size of the illuminating spot and the lack of importance of the size of the detectors. See text.} \]

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the horizontal magnitude of the tremor in a normal eye. This small amount of tremor effectively generates the waveform \( \Delta R \) without any other motion in the scene. Note that if the photoreceptors were twice as large, it would make no difference in the amplitude of the signal. However, it would make a difference in the signal to noise ratio of the system. \( \Delta R \) is the signal used to control the fixation point of the eye between saccades. It also plays a major role in the recognition of detail in the image presented to the eye.

### 15.1.5.6.1 The importance of serifs in legibility

If a real diffraction limited spot were used in the above figure and the actual shapes and spacings of the photoreceptors were used, the shape of the signals would be significantly altered. As the size of the original spot in the scene was reduced in size, the shape of the spot projected onto the foveola would become more rounded as shown on the left in Figure 15.1.5-2. It would approach the diffraction limited spot of the optical system alone. The signal level would fall below the noise level of the circuit quickly. By introducing serifs into the shape of small size type, the legibility of the type is considerably enhanced. The serifs essentially add high frequency pre-emphasis into the signal channel. This enhancement raises the peak signal to noise ratio slightly but, more importantly, maintains the signal above the noise level longer. This is very important when the signal, \( \Delta R \), is produced by subtraction. In such an operation, the signal level subtracts linearly but the noise level subtracts in quadrature. The result is a significantly poorer signal to noise situation. Small serif type faces are considerably easier to recognize at low light levels.

### 15.1.5.7 Signal to noise ratios

There are at least three distinct signal to noise ratios important in the vision process. The lowest and most basic is that required for detection of an event. The second is that needed to characterize an event, usually in terms of simple geometric features (parallel lines of a given spacing). The third is the level needed for recognition (alternately identification). The lowest level frequently involves simple serial data streams applied to a threshold. This threshold may be an RMS noise threshold or a more clearly defined circuit threshold. The signal to noise ratio required for characterization of a two dimensional image is clearly more complex, not necessarily higher numerically but involving some degree of correlation of the signal in more than one dimension. Recognition involves the most difficult to define criteria since it may actually involve not only comparison to a stored visual vector (engram) but other vectors (such as auditory).

### 15.1.5.7 Fundamentals of the organization of the nervous system

Guyton provides a description of the nervous system that can be outlined. The overall nervous system is usually divided into the skeletal-motor system and the autonomous system. The skeletal system is usually characterized as employing striated muscle tissue and using a single neuron to travel from within the spinal cord to its termination at an effector. The autonomous system, primarily controlling visceral functions and secretion, is usually associated with the vagus nerve. It is characterized as connecting to smooth muscle and involving at least one synapse between the spinal cord and the target destination. Within the autonomous system are the sympathetic and parasympathetic nervous systems. The motor muscles of the ocular sphere are commanded.
through the sympathetic system via nerves emanating from location T-1 of the spinal cord. The pupil, lacrimal glands and ciliary features of the eye are commanded through the parasympathetic system via nerves emanating from location T-3.

15.1.5.7.1 Redundancy, asymmetry and reliability

The visual systems of bilateral animals make a number of important tradeoffs to optimize the performance of the animal in its environment. One of the more interesting is the pairing of asymmetrical signal paths in order to obtain nearly symmetrical overall performance. This allows simpler techniques within the individual signal paths without a significant reduction in performance. A specific case is the asymmetry in the signal transmitted by the projection neurons controlling the pointing of the eyes. Because of the obstruction of the nose, each eye employs an asymmetrical signaling system that can command the eye to move in the temporal direction more promptly than in the nasal direction. However, since the other eye operates as a reflection of this condition, the overall servo system can command both eyes with the promptness of the more effective eye. In electronic amplifiers, this is called class AB operation. The system exhibits the quality of a class A amplifier when operating normally but upon a failure in one channel, the system operates in a degraded but adequate mode. The same situation is found in the individual chrominance channels but the asymmetry is not compensated. Thus, the S- and L-channels respond slower than the M-channel, resulting in a myriad of aftereffects related to moving or flickering scenes.

15.1.5.8 Types of memory

Neurobiology tends to define various types of memory based on performance. Two major types are explicit or cognitive memory and implicit or non-cognitive memory. Explicit or cognitive memory is associated with the recognition and/or recall of faces, places and facts. Implicit or non-cognitive memory is associated with habits. It is equally important to define memory in terms of physical memory techniques involved.

To understand the cognitive functions of vision, it is important to define a variety of forms of physical memory. These forms closely parallel the forms found in modern personal computers and digital television. At least three types can be clearly defined.

15.1.5.8.1 Long term or PROM memory

Long term memory exhibits similar properties to the programmable read only memory (PROM) of computers. It is a write once, read anytime type of memory. It is permanent and subject to recall at the will of the animal. It frequently suffers from inadequate indexing software with increasing age. However, this inadequacy can sometimes be affected by pharmaceutical preparations. It is large scale memory. The size of this memory may be effectively infinite if sophisticated overlay encoding is employed. This encoding method might be similar to modern spread spectrum frequency modulation techniques. There appear to be at least two conceptually different types of long term or Prom memory used in vision. The first, labeled PROM1, is large and incorporates a complex rule set. It appears to involve both genetically encoded and learned rules relating to danger. It appears to be organized to treat signals related to the vertical and horizontal plane separately. The smaller, PROM2, appears to be simpler, is probably entirely genetically programmed, and perform primarily housekeeping functions. It is similar to the simple character generator PROM in computers. It may or may not incorporate the code to produce the flick and tremor signals required by the Precision Optical System.

15.1.5.8.2 Medium or RAM memory

Medium term memory exhibits similar properties to the random access memory (RAM) of computers. This is

most likely present in a distributed form supporting a variety functional needs. In the case of remembering and recalling simple sequences, the size of the memory is distinctly limited and subject to erasure and reuse on a short term basis, minutes or less. It is frequently seconds for a seven digit telephone number. A. T. & T. performed significant studies on the recall time associated with telephone numbers of variable length in the 1950's. The size of this memory is quite limited compared to PROM memory.

15.1.5.8.3 Short term, scratch or cache memory

Short term memory exhibits similar properties to the cache memory closely coupled to the central processor of computers. In many if not all cases, the animal is not aware of this type of memory. In the visual system, it is a necessary element in motion detection since it allows the subtraction of a recently stored image from the current input image. It is also plays a key role in data compression prior to long term storage. It is probably also important to the re-creation of the large area characteristics of a scene within the cortex, ala a "PAINT" program of computer technology.

15.1.5.9 Inadequacy of many generic labels

The literature abounds in generic labels that lack specificity. Signal paths such as X, Y, Z, a, b, g, M & P were provided as placeholders by the initial electrophysiological explorers based on no model or on floating models. These designations become awkward to correlate to a more expansive model of the overall visual system and must not be relied upon. A similar situation occurred with the early psychophysical explorers who defined various ON-OFF, OFF-ON and similar designation. These designation refer ultimately to the dynamic aspect of the light level of the stimulant. OFF did not generally imply that all light was prevented from reaching the area of the retina under evaluation, only the variable part of the total stimulus.

The historical development of the adjective forms, ON-OFF, ON-Surround, OFF-ON, and ON-Direction, is understandable. However, use of these forms is no longer appropriate. They were developed based on examining action potential pulse streams under fundamentally abnormal operating conditions. Furthermore, their graphical presentation was frequently not comprehensive. This is because of the type of signal encoding actually used versus the type of encoding assumed by the investigators. First, the signals being examined were assumed to be luminance related. In fact, they are frequently the output of the first and second lateral processing matrices. These matrices operate in analog signal space and output biphasic signals where the polarity of the signals is related to their function. Under quiescent conditions, the ganglion cells associated with these biphasic signals typically exhibit a continuous pulse output stream of nominal pulse to pulse interval of 30 ms. (corresponding to an average frequency of 33 pulses per second (pps)). Under dynamic conditions, the pulse interval can be driven to as low as 10 ms. (an instantaneous frequency of 100 pps. Conversely, the interval can be extended to about 200 ms. (an instantaneous frequency of less 5 pps). In many graphics, this range is not properly displayed. A group of closely spaced pulses are shown resulting from the subtraction of two signals. If the inputs to the subtraction circuit were reversed, a similar set of widely spaced pulses would be obtained. However, the spacing would be nearly 20 times wider. This is difficult to show graphically. The words instantaneous and average are emphasized above to help stress the fact that the actual encoding is a type of phase modulation and not frequency modulation. Frequency modulation is the derivative of phase modulation with respect to time. Like any derivative, it can not represent the absolute value of the underlying signal nor can it describe an absolute input signal level. There is more information in the pulse stream than conveyed by its average frequency.
15.1.5.10 Conflict in the use of “tonic”

As the analysis moves closer to the brain, additional conflicts in terminology are found in the literature between the visual field and the brain research field. A particular problem is the adoption of the term tonic in brain research to describe a continuous series of action potentials. This is an inappropriate use of the term tonic as derived from electrotonic. A continuous series of action potentials is a normal characteristic of a free running oscillator as found in the differential channels of the nervous system. These differential channels are commonly associated with the chrominance and polarization type signaling channels.

In this work, tonic will continue to refer to a DC or slowly changing analog waveform lacking any oscillatory component.

15.1.5.11 Introduction of external feedback and mode switching

Previous Chapters have made use of a variety of signal manipulation techniques;

+ adaptive, logarithmic amplification,

+ logarithmic summation and differencing,

+ analog to pulse encoding in the temporal domain,

+ internal negative feedback

+ analog spatial encoding, of both the lossy and loss-free varieties,

among others. This Chapter involves the recovery of signals encoded by the above techniques plus the addition of at least three additional techniques. These are external negative feedback, mode switching and temporal signal differencing.
15.1.5.11.1 External (negative) feedback

External feedback is the return of a portion of the output signal of a circuit to its input by a path external to the fundamental circuit. The feedback can be negative or positive in polarity. Although the literature contains many models suggesting external negative feedback in the visual system, most of these are not compatible with the physical evidence when applied to a comprehensive circuit model. There are two clear examples of external feedback loops in animal vision. The first, and simplest, is the control of the optical aperture (via the iris) as a function of the incident illumination level. A more complex, and more important external feedback loop centers on control of the line of fixation. The line of fixation can be controlled, subconsciously, entirely in response to changes in the environment. It can also be controlled, subconsciously, as part of the cognitive process. Finally, it can be controlled, willfully, by the organism. The mode of control in effect at a given time is subject to a pre-programmed, possibly genetically controlled, set of rules.

To completely understand and evaluate the use of external feedback in vision, one must use the methods of sampled data control system analysis. However, the general rules applicable to the external feedback found in vision are the same as for conventional analog signal feedback systems.

15.1.5.11.2 Mode switching

To appreciate the operation of the cognitive functions of vision, it must be recognized that the system operates in a variety of modes. Most of these modes are transparent to the conscious animal. Depending on the rules determining the instantaneous operating mode, the brain may accept or ignore signals received via a given signaling channel. This mode programming is most apparent in the large saccades and a critical tool of the magician. Although man can willfully control the line of fixation a majority of the time. He has no control over it during the presence of an imminent external threat. Furthermore, he is not even aware of the fine variations in the line of fixation related to the perception function (see definition of perception).

The individual modes of importance to vision will be discussed in later Sections.

15.1.5.11.3 Temporal signal differencing

One of the key processes used extensively in the perceptual aspects of vision is temporal signal differencing, the basis of mathematical differentiation. The name is descriptive. By comparing a signal received at one time with the previously received signal applicable to the same region, a temporal change can be computed as a function of time. If this change is with respect to spatial position, it is defined as a velocity in spatial coordinates and reported as a movement of something in the image field. If the change in the spatial field does not involve a change in spatial position, it is most likely a change in luminance amplitude during a “frame interval.” The cognitive system uses such a change to extract the critical information from a scene without requiring the entire scene to be analyzed again. It assumes the remainder of the scene has not changed and that it can rely on the short term or long term memory for information about the great majority of the illuminance values of the scene as a function of spatial position. This is a very important capability of the vision system.

15.1.6 Coordinates of the old brain in human

There is considerable difficulty for a layman in neuro-anatomy attempting to correlate the research related to the role of the old brain in vision. Many books on comparative anatomy are actually compendiums that leave most of

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the comparative activity to the reader. The problem is due primarily to the significant role evolution has played in this area. Even among chordates, there are significant differences between man, the other primates, and the lower chordates (even the monkeys). As the topology has become more complex, so has the topography. Feldon, et. al. took the view that retinal specialization rather than phyletic status is the principal determinant of the old brain projection. Because of these differences, different names have been assigned to the structures in each type of brain.

15.1.6.1 An evolutionary mapping

The old brain of all animals has been known to play an important but poorly understood role in vision (as well as other sensory activity) for a long time. Each generation of investigators has resolved the old brain into finer divisions as knowledge increased. Unfortunately, workers in different fields adopted different morphological designations for functionally similar features. Both geometrically descriptive and fanciful names have become prominent. This situation has been aggravated by both the three dimensional character and the plasticity of the old brain. The general flow begins with the old brain, as a global entity. It has been divided into three main portions usually labeled the thalamus (diencephalon), the midbrain (or mesencephalon) and the pons. An obvious morphological feature in early work was the roof-like feature (tectum) of the dorsal thalamus. The portion of this structure related to vision came to be identified as the optic tectum or the pretectum. An optic tectum has been identified in nearly all animal families and species as noted in Vanegas. However, this designation is not commonly used in humans and other primates because of the additional degrees of differentiation encountered. In the higher chordates, this structure was found to exhibit wings that were important to vision and they became known as the lateral geniculate bodies, LGN. Initially the medial geniculate body was assigned a major role in hearing. With further analysis, an additional portion of this medial structure was found to be important to vision. It came to be known as the pulvinar in human anatomy but remained associated with the pretectum in lower animals. The pulvinar was found to be closely associated with two other nuclei known as the lateral posterior nuclei. This area will be addressed further in Section 15.6.

For purposes of this work, the complex consisting of the pulvinar and the various geniculate nuclei will be considered synonymous with the pretectum of the lower animals. Each of the above elements can be considered a feature extraction engine just like those associated with the cortex (or new brain).

A separate and distinct feature of most species is the superior colliculus, SC. It is primarily associated with the mid-portion (or mesencephalon) of the old brain. Functionally it is quite distinct from both the LGNs and the PGN in all species. While the SC performs complex signal processing, it is not a feature extraction engine. It is a major element in the command generation path of the visual system. In that role, it synthesizes efferent commands. It does not analyze afferent signals.

The superior colliculus, SC, appears in most animals whether foveal or afoveal. In the foveal animals, there is a clear distinction between the superior colliculus and the LGN and PGN, portions of the thalamus. Both the differentiation between the PGN and the LGN and the level of development in the pretectum is more pronounced in man than in the other primates. It is the PGN/pulvinar couple in man that is the key to his ability to read.

15.1.6.2 A global introduction to the old brain in human

As noted in the heading, this section is an introduction prior to a more expansive discussion in the next section. Before proceeding, the reader may wish to review the introductory remarks in Section 2.3. It provides a large bibliography. For purposes of this section, [Figure 2.3.1-2] is reproduced here as Figure 15.1.6-1. Note the

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separation of the optic nerve posterior to the chiasm into two distinct portions as it enters the old brain. It is important to note the close physical relationship between the pulvinar portion of the thalamus and the superior cerebellar peduncle (part of the internal capsule). Also note the location of the ophthalmic nerve leaving the pons in the area of the oculomotor nuclei. These elements are critical to the high speed operation of the POS in both servo-control and in creation of interps and percepts. Not shown in this old figure is the critically important thalamic reticular nucleus that forms a thin covering over much of the thalamus. Much of this covering has a woven appearance. This element will be addressed in detail in Section 15.6.2.
Figure 15.1.6-1 CR Caricature showing the position of the Pulvinar, LGN and Thalamus in relation to the old brain. Note the rostral part of the thalamus is to the left. The optic nerve (commissure) merges with the brain at a caudal location. Note also the separation of the commissure proximal to the optic chiasma into two separate bundles going to the LGN and to the brachium and Superior Colliculus. Note further the close relationship between the superior cerebellar peduncle and the pulvinar region. From Mettler, 1948.
There is a considerable problem with this figure at the research level. First, the thalamus is far from ellipsoidal and has areas of bilateral symmetry and other areas that appear to lack this feature at the functional (signal processing) level. The individual portions of the surface associated with different functions exhibit different textures that are difficult to reproduce in an artist’s rendition. The following sections will show, it is nearly bifurcated by other structures and extremely difficult to image without relying on three-dimensional techniques.

Blinkov & Glezer have provided a large tabulation of the features of both the brainstem and the cerebral cortex of the human brain75.

15.1.6.3 Expansion of the topography of the LGN/PGN region of the thalamus

The artistic rendition in the previous figure shows the optic nerve bifurcating morphologically just as it enters the thalamus. A major cross-section of the nerve is shown projecting to the lateral geniculate nucleus (LGN). A smaller portion is shown projecting to the superior colliculus and the brachium, or arm of the superior colliculus. The medial geniculate nucleus (MGN) is shown close by and associated with the brachium of the inferior colliculus. Figure 15.28 of Carpenter & Sutin provide a different identification76. They show the optic nerve bifurcating with the major portion proceeding to the LGN and the minor portion terminating at the surface of the pulvinar, i.e., the location of the PGN. Figure 15.1.6-2 from Noback describes this area in greater morphological detail77. The brachium of the superior colliculus is shown adjacent to the visual lateral geniculate nucleus. The brachium of the inferior colliculus is shown adjacent to the auditory medial geniculate nucleus. Noback identifies the neurons within these brachium as related to the visual and auditory systems respectively. However, he does not offer any reason for these afferent neurons to be connecting to the efferent oriented superior colliculi (known collegially, along with the inferior colliculi, as the quadrigemina).
These two morphologically identified features on the surface of the brachium are defined here physiologically as the perigeniculate nucleus of vision and hearing respectively. They receive afferent neurons from the peripheral sensory organs and produce output afferent neurons directed to the pulvinar immediately forward. It is proposed that few if any neurons project from the PGN’s to the quadrigemina.

Topologically, the neurons of the optic nerve project an image of the instantaneous visual object space in analogy with the monkey as illustrated in Figure 15.1.6-3. This figure has been extended to show a distinctly separate PGN. This structure may or may not be identifiable in monkey. However, its role in humans is major. The vast majority of the neurons of the right visual hemifield (approaching two million) are rearranged by computational anatomy to project on the left LGN as shown. The small number (23,000) of neurons associated with each reticulocellular pathway project to their respective PGN shown as located medial to and adjacent to the LGN. As discussed in Section xxx, the LGN is folded to form multiple layers that are spatially aligned with each other. This alignment facilitates the merging of the parvocellular and magnocellular neurons as part of the stereopsis mechanism. The PGN is likely to be multilayer also but with a different topological structure designed to facilitate associative correlation, possibly over several image acquisition cycles. In performing their stereopsis task, the retinocellular neurons of the PGN operate differently than those of the LGN. While, Carpenter and
Sutin did not specify the role of their three putative classes of ganglion neurons projecting to the thalamus, this work proposes that these are the parvocellular, magnocellular and reticulocellular neurons following paths with those same designations on their way to the thalamus.

Functionally, about 23,000 neurons in this nerve proceed to the perigeniculate nucleus (PGN) located medial to the LGN. These neurons form the reticulocellular pathway to the PGN.

Malpeli & Baker have provided voluminous data on the representation of the visual field on the LGN of *Macaca mulatta*.

15.1.6.4 The old brain of human at the research level

The vision community appears to have oversimplified its view of the old brain, and thereby slowed understanding. The portion of the old brain of interest in vision is largely confined to the diencephalon. It is that portion of the old brain near the top of the spinal chord that is surrounded by both the major commissure interconnecting it with the cerebrum and the major commissure interconnecting the two hemispheres of the cerebrum. It is also surrounded by a complex vascular plenum. Sundsten, illustrating the latest volume by Nolte, has provided a three-dimensional representation of this area. The continuing relationship between Sundsten and...

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Nolte has provided a new, and frequently updated interpretation of the brain that supercedes all work in the field prior to 1995.

As discussed in Section 2.3.1, the top of the brain stem blossoms in a very complex way, not unlike a flower matures at the top of a stem. In a sense, the buds that mature into the cerebral hemispheres and the cerebellum form large sheets of material that are paper thin. These are folded repeatedly to provide maximum total area within an available volume. Both of these structures are fundamentally planar. The elements of the diencephalon are fundamentally different. These structures have a three dimensional character. They are bulk structures. Because of this feature, they contain immense numbers of neurons within each element.

The “flowering” of the diencephalon involves more than one type of element. Very significantly different elements are:

- The thalamus.
- The inner (internal) capsule
- Potentially several layers surrounding the thalamus.
- Potentially elements, or extensions of the amygdala.
- The fornix.

An alternate description divides the diencephalon into the epithalamus, subthalamus, hypothalamus and thalamus. For the moment, the above list of elements will be explored. Kretschmann & Weinrich have provided a caricature of these elements in their figure 43. However, the several layers surrounding the thalamus were not portrayed at the scale used. Mishkin has also provided a caricature of several of these elements with somewhat less focus and a broader context, but does not cover the full breadth of the intricate entanglement of these elements. The caricature supports calling the structures surrounding the thalamus a corona.

The thalamus is one of the larger and more compact elements of the diencephalon. However, its physical structure is quite complex. When examined at a distance in the lateral projection (with the cerebrum removed), it appears to be ellipsoidal. However, when viewed from above, it appears to be nearly completely bifurcated, except for a posterior section. Each bifurcation is frequently called a thalamus as if the other was totally absent. Each of the bifurcated elements is divided into several distinct compartments by an internal medullary lamina. This lamina includes nodes of neurons (engines) in its own right, just like the peripheral compartments. Nolte describes these engines as intralaminar nuclei.

While used variously in the literature, Nolte defines the internal capsule, rather than the inner capsule, as a commissure located between the nearly bifurcated portions of the thalamus. Because of the complexity within the area of the diencephalon, the internal capsule also has a very complex shape (Nolte, pp 403-5). The internal capsule plays a role within the diencephalon not unlike the role of the corpus callosum, the main mass of commissure mentioned above. It connects the thalamus, the fornix, the amygdala and the other layers associated with but independent of the thalamus. Nolte describes the internal capsule as called the corona radiata as it emerges from the cleft between the two parts of the thalamus. As it emerges below the cleft, it is described as the cerebral peduncle.

The thalamus is occasionally described as possessing an outer layer known as the external medullary lamina. It is

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also frequently considered to have a next-outer layer surrounding the upper two-thirds of its area called the thalamic reticular nucleus. These layers are frequently separated from the thalamus by significant commissure bundles. While Nolte lists the reticular nucleus in their table of the subdivisions of the thalamus (and stress it is different from the brainstem reticular nucleus), he does not describe it further or provide an abbreviation for it in that work. He appears to largely discount the functional importance of this layer (page 381 in 4th ed., 396 in the 5th).

The complex and convoluted entwining of these structures makes it difficult to assign ultimate origins to these various layers. No discussion could be found that showed the morphogenesis of them and explained the reason for the fundamental differences in their topographic and topologic structures. However, it is clear from the literature that these elements all play a significant role in the higher level processes that determine the mood, the memory and the smoothness of motion of the organism. In this context, these outer layers of one author may be the fornix and amygdala extension of another. Until the fornix, possible extensions of the amygdala, external medullary lamina and thalamic reticular nucleus are more clearly differentiated, the functional characteristics of the thalamic reticular nucleus will be considered typical of the group.

Many, if not most, texts dismiss the thalamic reticular nucleus (TRN), strip it away in their illustrations, and focus morphologically on the thalamus. This focus has led to an excessive emphasis on the thalamus without concurrent progress in determining the main functional mechanisms within the thalamus.

The above approach has also led to an oversimplified view of the role of the inner capsule. The recent trend has been to describe the role of the thalamus in terms of a relay and an association role. The word relay is phonetically convenient but appears to be too simple, and too suggestive of a narrow role, to be satisfactory.

Topographically, the TRN is more an outer lamina than a nucleus. Its topological arrangement is also more akin to a lamina than a nucleus. This work will show that the thalamic reticular nucleus enshrouding at least the upper two-thirds of the surface area of the thalamus, is a fundamental functional element in the signaling processes occurring within the neural system. It is one of the most important of these functional elements and deserves greater prominence. The TRN is essentially a terminus of commissure originating in the thalamus and of commissure originating in the cerebrum. Very few neural pathways can be traced between the cerebral cortex and the thalamus by dye techniques because of this barrier between them.

Nolte appears inconsistent with respect to the neural pathways associated with the TRN. While Nolte says there are no neural paths between the TRN and the cerebral cortex, he says there are such paths between the intralaminar nuclei and the cerebrum (Chapter 16 outline). Later, on page 402, he shows collaterals terminating in the TRN of neurons that originate in either the thalamus or the cerebrum. On the other hand, Robinson & Petersen describe pathways between the dorsomedial region of the pulvinar and area 7 of the cerebrum. Such paths would logically pass through the TRN which surrounds a majority of the thalamus (and essentially all of the pulvinar), particularly in the direction of the cerebral hemispheres. Other authors have claimed that there are virtually no neurons that pass through the TRN. They claim virtually all neurons associated with a given path terminate in the TRN where they are processed or regenerated prior to continuing to their ultimate destination. The question may come down to whether the element of a given neuron occurring within the TRN is a synapse or a Node of Ranvier.

It is the group of elements surrounding much of the thalamus, the TRN, external medullary lamina, fornix and amygdala extension that are closest to the essence of thinking in humans. For simplicity, they can be grouped and considered the corona of the thalamus. They appear to provide the primary seat of coordination with regard

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to the operation of the overall central nervous system. In this role, the TRN does more than relay signals, it distributes signals. It distributes these signals in a largely arbitrary, and highly flexible, way in accordance with its own internal computational processes and memory. The computational processes can be considered associative. However, they are more than that. The processes occurring within the TRN are correlative. They extract information with respect to patterns. These patterns may be visual, aural, tactile or combinations of the above. These combinations are assembled into at least an initial version of a saliency map describing the environment surrounding the organism.

As will be developed in Section 15.6.1 & 15.6.2, the elements of the corona form the primary signal distribution and signal correlation subsystem in the nervous system. In this role, they dynamically control the distribution of nearly all signals from the peripheral nervous system, including visual and aural inputs, and correlates the information in order to extract the relevant information. Having extracted the relevant information, it controls the operation of the oculomotor and skeletal motor systems. It controls these systems in order to avoid threats to the organism as well as to acquire additional relevant information. It also passes this information, after processing into a higher level “machine language” on to the higher cognitive processes. Quoting Nolte & Angevine, “... the thalamus is the site where decisions are implemented about which information should reach the cerebral cortex for further processing.” At a deeper level of differentiation, this work will show it is the TRN and other members of the corona that implement and control the flow of information. The thalamus will be shown to be a large scale memory unit containing multiple areas of PROM type memory. Its role is to support the higher level computational and control functions of the corona.

The importance of the corona, in conjunction with the thalamus and cerebellum, is seen in Bentivogio, et. al. They stress the critical nature of any injury to these elements. The primary result is a condition known as global anterograde amnesia. It is marked by “failure to retain new sensory and other cognitive information beyond the period of the immediate memory span.” It is also suggested by these authors that such injury can involve loss of the ability related to “acquisition of habits and other sensorimotor skills.”

15.1.6.5 Mapping of the pulvinar in humans

A leader in the study of the pulvinar is Chalupa. As late as 1991, he includes a paragraph title: “What Does the Pulvinar Do?” without providing a substantive answer. He does provide a list of functional features associated with the pulvinar and a comprehensive bibliography. Chalupa addresses the fact that the size and differentiation of the pulvinar increase markedly as one ascends the evolutionary scale. He describes the pulvinar as the largest nucleus in the thalamus and recognizes its role in extrageniculo-striate visual communications. However, he does not address the pulvinar as part of the POS although he speaks extensively of the lateral posterior nucleus, LP, pulvinar complex and its connections to the extrageniculate thalamus.

A major problem has been the precision of the probing of this area designed to determine the fields in object space associated with different areas of the pulvinar and associated bodies. The probing has generally lacked geometric precision and little or no attempt at temporal differentiation (particularly with a precision below three milliseconds in humans and a smaller number in smaller animals) has been made. This work provides a more comprehensive description of what the pulvinar does and why.

Carpenter & Sutin have recently provided a highly illustrative view of the thalamus and its subdivisions. However, Steriade, et. al. have provided a significantly different view. They are presented, along with a third

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caricature, and discussed in Section 15.6.1.

15.1.6.6 Mapping of the superior colliculus

The superior colliculus of the human has not been explored significantly because of the inaccessibility of the organ and its presence within the POS servomechanism. Historically, the superior colliculus has been assumed to receive signals from the retina because of its response to signals from the retina. The assumption has been that the superior colliculus was a stage 4 element. However, this is largely erroneous. The superior colliculus is a stage 6 element involved in the response of the organism to a stimulus after processing within the CNS. However, it is within the POS servomechanism. It is the element controlling the operation of the oculomotor neurons and muscles (along with nearly all other motor neurons and muscles).

Recent papers concerning the superior colliculus are reflecting its stage 6 function. While nearly all of these papers relate to the cat, a few relate to the monkey.

15.1.6.6.1 Mapping of the superior colliculus in monkeys

Everling et al. have provided good data on the superior colliculus in monkeys86. The significant delay between the stimulus of the POS and the beginning of the response recorded in the superior colliculus is indicative of the time consumed in neural signal manipulation before a response is decided upon.

15.1.6.6.2 Mapping of the superior colliculus in cats

Figure 15.1.6-4 shows a mapping of the superior colliculus of the cat by Feldon, et. al87 that has been widely reproduced. It is important to review the original article and compare the technique used against the model of this work (See Section 15.6.5). While the clinical technique was elegant, by suturing the eye to the conjunctiva, they effectively eliminated tremor from the experiment. This resulted in the visual system only being sensitive to changes in object space. Their focus was on probing the superior colliculus at 0.5 mm intervals in an orthogonal array projected onto the surface of the body. Attempts to probe at a constant depth were thwarted and a variance of 1.5 mm was encountered. This value far exceeds the thickness of a single multilayered neural surface. A majority of the readings were believed to be from the strata known as griseum superficiale. A black bar was moved within the field of view to determine the approximate field of view associated with a given probe location. This technique did not provide precise information relative to the foveola. They did not maintain any temporal coherence between their test image and the time of neural response. Although they speak of the signals as being a response to the stimuli from the retina, the superior colliculus does not respond directly to input stimuli based on this work. It is primarily an element of the command path receiving its inputs from both the pretectum and the higher cognitive centers and driving the oculomotor neurons. The signals recorded in this study were probably related only to the low temporal frequency section of the POS.

Their discussion centers on the likelihood of a dual projection for a small retinal sector located near the area centralis region of the vertical meridian. This position confirmed that of other investigators and is consistent with this theoretical work. They discuss the complexities associated with this dual projection and recognize that the signals from the two eyes follow a combination of crossed and uncrossed paths depending on the projection. These paths correlate with the analysis paths and awareness paths of this work. They also note the considerable expansion of the relative area of the superior colliculus associated with the area centralis (foveola). They speculate about the relative importance of the crossed (awareness) and uncrossed (analytical) paths in cat

The figure displays a map of the superior colliculus as seen from “above” for the contralateral temporal and ipsilateral nasal fields. The shaded area rostral to the vertical (0°) meridian constitutes the representation of the contralateral nasal field and lacks binocular overlap. Based on the superior colliculus being in the command signal path, this view cannot separate the signals arriving via the analytical (uncrossed) and awareness (crossed) paths.

Additional sources related to the cat superior colliculus include the Fuchs team in Seattle88,89.

15.1.7 Coordinates of the human cerebral cortex, or neo-cortex

A comprehensive review of the electrophysiology of the visual system is very difficult without a physiological mapping of the cerebral cortex. Unfortunately the usual obstacle appears, there are many such mappings supported by different schools. Nolte90 has provided a “tree” of the central nervous system and an accompanying sketch in one figure that is quite useful with three limitations. It does not show the ocular globes and it does not stress that the temporal lobe extends along the exterior surface of the cerebral cortex to an intersection with both the occipital and parietal lobes. It also omits the fact that the Temporal and Parietal lobes contain significant engines associated with vision. It is suggested that his figure 3-23 be expanded to show the ocular globes and to introduce a third breakdown, the ocular globes, along with the brain and the spinal cord under the heading Central nervous system. Nolte also provides multiple lists defining the different morphological features of the human brain. Brown91 has provided annotated top views of the human cortex based on earlier versions from Kandel & Schwartz. Heide, et. al. writing in Becker, et. al. have provided a profile view of the human brain based on fMRI experiments92. Unfortunately, a printing error omitted many of the labels in the figure. This type of projection will become quite common in the future because of the ease of experimenting with the fMRI. These authors also provide a comparison of the location of many of their labeled areas with the areas of Brodmann.

Blinkov & Glezer have provided a large tabulation of the anatomical features of the cerebral cortex93.

15.1.7.1 Coordinates in the plane of the cortex surface

According to Noback94, using the term cytoarchitectural criteria, Campbell parceled the cortex into 20 areas, Brodmann 40 areas, von Economo 109 areas and Vogt over 200 areas. This listing does not include listing of the

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visual areas under the more recent V(n) system of notation nor the map of Bailey and von Bonin of 1952. Bailey and von Bonin have provided a broad atlas of the different maps, except theirs. The most coarse discussion of the cerebral cortex as it relates to vision usually starts by discussing the striated cortex, a large area at the posterior of the occipital cortex. The next finer divisions are usually those of Lund, followed by those of Brodmann. Unfortunately, none of these systems provides an adequate representation of the area occupied by the folds of the human brain. It appears that the most commonly used systems are those of Brodmann and Lund. However, this still leaves two systems that are not completely compatible, are not particularly precise as to boundaries and have not been extended to greater accuracy through decimalization or some other technique. In the case of the medial surface map of Brodmann, the numbered areas are not necessarily continuous individually nor are adjacent numbers necessarily assigned to adjacent areas. The early numbering system did not adequately account for the many folds in the human brain. This situation is making further correlation between the monkey and man ever more difficult. In 1983, a new system appeared in conjunction with a new clinically based dual pathway system of vision. This system used a series of two and three letter abbreviations different from those in the next section. It evolved into a system that attempts to correlate with the Magnocellular and parvocellular pathways of vision and is apparently oblivious to the pulvinar pathway. There is no current system that provides a contiguous transform between the areas of the monkey paleo- or neo-cortex and that of man at adequate grid resolution.

Zeki & Marini have provided side by side top views of the human and macaque brains and labeled similar structural features. The additional amount of folding in the human brain is obvious. What is not obvious is that some of the folding is of such depth that entire areas of the brain are not visible in side or top views (such as zone V3). Maunsell & Newsome have provided cut-away views of the monkey brain in an attempt to illuminate these hidden areas. They also provide a map of the entire occipital cortex of the monkey using conventional map-making techniques but without providing the precise projection technique used. A similar map of the human cortex is obviously more difficult to prepare. Such a map of the occipital lobe of human was recently prepared by Tootell, et. al. using the latest computer techniques. See Section 15.2.5.7.4.

The best illustrations of the human cortex showing Brodmann’s numbers was found in Pansky, et. al. Their page 205 from Penfield & Rasmussen is reproduced as Figure 15.1.7-1. It illustrate clearly the non-contiguous nature of Brodmann’s numbers and the location of the small areas 3, 1, 2 & 5. A useful view of the human brain from below with Brodmann’s notation appears in Young. Young also provides top, side and saggital views with both common names and Brodmann’s notation shown. One can see clear cases of “artist’s license” when comparing this figure to that of Noback. There is more modularity in the above figure and Area 12 does not appear in Noback at all. Only reference to Brodmann’s original paper can insure an accurate representation of his notation. Page 213 in Pansky, et. al. provides a brief correlation of the functional designations, AI-AII, MsI-MsII, Sml-SmII, & VI--VIII with A for auditory, Ms for motor-sensory (areas anterior to the central sulcus), Sm for sensory-motor (areas posterior to the central sulcus), and V representing visual.

Fuster has provided a large number of comparisons between the brains of different species. These comparisons show his view of equivalent areas of the brain. He has also provided additional annotation concerning the areas specialized with respect to different sensory and motor modalities. The figures aid in identifying the “prefrontal cortex” defined by Fuster. He initially defines this area anatomically as receiving projections from the

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mediodorsal nucleus of the thalamus. Unfortunately, he then waters down the definition based on the currently limited understanding of the role of the mediodorsal nucleus. He also accepts that “the prefrontal cortex is also connected to many other cerebral structures.”
Figure 15.1.7-1 Brodmann’s areas showing their discontinuity in numbering. From Penfield & Rasmussen, ( ).
The problem is complicated by the frequent use of lower primates, even old world monkeys, in laboratory investigations. There are significant differences in the location of functional areas, engines in this work, of the brain among these species relative to the major sulci (compare Zeki’s maps of the macaque monkey and maps of the human by Noback or Penfield & Rasmussen). There are even greater differences between the human and the so-called new world monkeys. A major difference is the importance of area 7 and the Pulvinar pathway to the great apes and man. Zeki largely ignores area 7 of the human brain in his 1993 book\(^\text{102}\). This area and routing is functionally trivial in lower species. Nolte has provided an easily accessible listing of the sulci and gyri by name\(^\text{103}\). Bailey and von Bonin have provided an even more complete set of tabulations and figures defining these features\(^\text{104}\). McKeefry & Zeki have provided a clear description of several sulci of the human brain looking from above\(^\text{105}\).

The central sulcus of the human brain is usually taken as the dividing line between abstract thought and sophisticated perception, and the lower functions of sensory mapping and initial perception associated with the safety of the animal. Anterior to the central sulci are the frontal visual fields, area 8, which are known to control the voluntary actions of the eyes. Stimulation of the dorsal portion of area 8 causes the eyes, head and skeleton to turn in the contralateral direction. Stimulation of the ventral portion of area 8 only causes the eyes to turn in the contralateral direction (Pansky, et. al provide a brief summary of responses due to stimulus of the visual centers\(^\text{106}\)). These actions are usually thought to involve assimilation of the commands from area 8 with other command information from area 5 in a motor control region of area 7a. Area 7a is usually defined as the anterior portion of area 7. The motor control commands from area 7a are passed to the super colliculus for further assimilation with information from the vestibular system before forwarding to the oculo-motor neurons. Area 5 (not to be confused with V5) receives information from the occipital, parietal and (inferior gyrus of) the temporal lobes. Each of these lobes contains at least 6-10 engines associated with the visual process. Area 39 probably collects information from multiple individual engines of the visual system and passes the command fragment to area 5. Stimulation of area 39 is known to cause the eyes, but not the head or skeleton, to turn in the contralateral direction.

Within areas 17,18 & 19, a number of the engines associated with remapping and initial perception of the visual field have been extensively explored. To aid in this process, a simple numbering system based on the sensory system involved and a single following digit (usually Roman in general neuroscience but frequently arabic in visual research) is used. The visual numbering system, V(n), has matured over a number of years. V1 was first used to specify the zone known as as the primary visual cortex. This zone is apparently coextant with area 17 of Brodmann and exhibits a unique surface quality, striation. Soon areas V2 and V3 were defined and then subdivision such as V2a and V3a. Zeki has played a central role in defining V4 and V5\(^\text{107}\) however much of his work has been with monkeys. Their brain is significantly different from that of humans with regard to vision, particularly concerning the analytical functions.

V1, or Area 17, is the only area considered to have a surface that is striated. The remaining anterior portion of the occipital lobe beginning with area 18, is usually labeled prestriated.

### 15.1.7.1.1 Correlation with topographic areas of monkeys

Zeki has provided extensive studies on the location of elements of the visual system in the brains of rhesus monkeys. He considers area 18 of the macaque, and the sulci associated therewith, to include V2, V3, V4 and V5. The illusory nature of these designations is illustrated in figure 8 of the above Zeki paper. Tovee has

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presented a similar figure that aids in the correlation of the terms used by different schools of investigation\. By comparing the above works and the following reference to Maunsell and Newsome, the general relationship between the various V\# areas and the similarly arranged alphabetical designations can be seen.

These designations are based primarily on a horizontal slice through the brain of a macaque monkey as shown in Figure 15.1.7-2. A larger problem is that these visual zones do not appear in the same positions relative to the sulci when other slices are taken through the cortex. Nor are the sections through the left and right hemispheres of the posterior half of the cortex symmetrical. Zeki notes that V2 is associated with the posterior wall of both the lunate and inferior occipital sulci of the macaque and probably on the surface of area 18 in the absence of these sulci. The result is a clear demonstration that the engines of the cortex do not correlate with the sulci or the gyri (tectonic plates) of the surface of the cortex. The “form” of the cortex has little to do with the detailed functional nature of the cortex. The exact locations of the equivalent engines on the surface of the human cortex are less precisely known. The names of the similarly located gyri and sulci of human can not be matched one-to-one with the macaque.

Maunsell and Newsome have also provided a number of figures illustrating the visually important parts of the cerebral cortex of macaque\. In their introduction, they equate the striate cortex and area V1. Figure 15.1.7-3 presents an early attempt at a surface projection for the right hemisphere of the macaque monkey. The areas are meant to be representative of their actual location and size. The authors did not describe their projection in specific cartographic terms. However, they did in an earlier paper discussed below.

The new elements appearing in the figure are labeled as follows:

- 7a
- V1 – (area 17)
- V2 – (area 18 and the parietooccipital sulcus)
- V4 – (area 19)
- AIT – Anterior inferior temporal area, (?_area 20)
- CIT – Central inferior temporal area, (?_Area 21)
- LIP – Lateral inferior temporal area
- MST – Medial superior temporal area (?_Area 22)
- MT – Middle temporal area
- PIT – Posterior inferior temporal area, (?_Area 37)

\begin{figure}
\centering
\includegraphics[width=0.5\textwidth]{figure15.1.7-2}
\caption{Location of V(n) based on a horizontal slice through the brain of the macaque monkey. (a); the occipital lobe is to the left. (b); the shaded represents V1. From Zeki (1993)}
\end{figure}

PO – Parietal-occipital area,
PS – Parietal striated area
STP – Superior temporal polysensory area

Van Essen & Maunsell discussed the problem of developing a planar map of the cortex of the primates and their close relatives\footnote{Van Essen, D. & Maunsell, J. (1980) Two-dimensional maps of the cerebral cortex. J. Comp. Neurology, vol. 191, pp. 255-281}. They worked primarily with old world monkeys, cercopithecus and macaque, and cats. The results are very useful but not entirely applicable to humans. They discussed the nature of the cartographic problem of creating a useful map of the cortex in the language and techniques of the non-cartographer of the 1980’s. However, the steps taken can be related to more precise terminology used in that discipline. The authors goal was to achieve an equal area mapping by methodically unfolding an actual cortex, making selected cuts where appropriate, and then tracing the images of contour lines in photographs of the original cortex using tracing paper which allowed for forshortening but not lengthening of individual lines. Although they confirmed the relative thinness of the cortex relative to its area, they also noted the severe folding associated with some of the sulci. Based on the finite thickness of the cortex and the curvature, they chose to consider the fourth layer of the cortex as the most appropriate layer to map.

Because of the significantly different curvature of the occipital lobe, it was treated differently. The overall result was a map combining two distinct projections, one of which was interrupted. The authors attempted to maintain equal area at the expense of angular position accuracy (the maps were non-conformal). However, their technique also introduced deviations that were not characteristic of either a rhumb line or a great circle. Their technique did not employ a true, or mathematical, projection but attempted to trace an actual curved surface into a flat plane according to a set of procedural rules.

Their technique resulted in a combined interrupted non-conformal equal area map of an entire hemisphere of the cortex they estimated to be accurate in area to within 20% of the actual hemisphere. The angular distortion frequently reached 60° and averaged near 20°. The map did not require any interruptions in critical topographic areas. The authors equated this fact to the relatively uniform curvature of the basic hemisphere. They did note their concentration on the visual portions of the cortex and the possible need for additional interruptions if higher precision was desired in the parietal and temporal areas. Their presentations show the location of both the nominal centerline of major sulci as well as the general area included within the sulci. In several cases, they showed that a single point appeared at three locations along the interruptions of their map. This point has been added to Figure 15.1.7-3 along with labels along the two edges to aid orientation of the reader.

It appears that a map of more quantifiable precision can be achieved by employing standard projection techniques employing planes, cones and cylinders. It also appears that a conformal result would be highly desirable. Tootell, et. al. have recently created a high quality planar map of the human occipital lobe using the latest computer programs.

VIP– Ventral intraparietal area
VP– Ventral posterior area

[Add notation for figure if avail from Maunsell]
based on the techniques of formal topography\textsuperscript{111}. It has not yet appeared in an atlas form. The computer processing is extensive and significant. However, it is focused on the location of V4 and other image processing engines beyond V1. As such, it makes a cut along the calcerine fissure and then flattens the two pieces of cortex above and below this cut. An alternate would be to keep the surface of V1 contiguous and make the cut along the margin just beyond the vertical axis. See Section 15.2.5.7.4. The margin would consist of a portion or all of V2. This representation would maintain greater similarity to the macaque representation in Section 15.2.5.7.1.

Van Essen & Maunsell noted the variation in location of the sulci between animals of the same species as well as across species lines. For precise work, it is clear that species specific maps are necessary and that individual maps should probably be given individualistic names. This would allow comparison between new maps of specific subjects with a nominal standard. Such comparisons are liable to become meaningful with the advent of the ability of discerning the size of a given cortical engine as a function of the innate ability of a subject with respect to spatial, musical or other generic classes of information.

The Van Essen & Maunsell paper provided a series of overlays allowing a convenient comparison of the notation of Brodmann versus Bailey & van Bonin. The Mausell & Newsome paper provided a similar figure showing the location of the visual areas as well as more detailed notation as shown in the above reproduction.

Recently McKeefry & Zeki\textsuperscript{112} have also discussed the variability in the location of V4 in human. The discussion is with respect to various gyri and sulci rather than an absolute position on an unfolded two dimensional surface. Tootell & Hadjikhani go into much greater depth based on fMRI techniques to explore whether a dorsal component of V4 even exists\textsuperscript{113}. Both discussions use the stereotaxic coordinates of Talairach & Tournoux\textsuperscript{114}. The variability of location on the surface of the human brain is very large. They say the location of a given voxel (a cortical response to a given visual stimulus observed by fMRI techniques), related to V4, can vary by 34 mm along the anteroposterior (y) axis in the left hemisphere and as much as 30 mm in the right. Interestingly, they claim V4 is invariably found on the lateral aspect of the same sulcus in spite of the above variations in absolute position relative to the brain case.

Talairach & Tournoux provided a new atlas in 1993 that continues the rectilinear stereotaxic approach\textsuperscript{115}. Their figure 1 provides a good representation of the coarseness of the approach of using long needles in a rigid frame to establish locations within a brain prior to its detailed surgical examination. Their remarks on page 12 are useful in discussing the adequacy of either sectioning or of sectioning after establishing locations with both parallel and orthogonal needles compared to the detail level available from MRI (currently at the 1mm slice thickness) and other techniques. Writing in the 1950's, they note the situation will certainly change when better volumetric reconstruction techniques appear, and the variability of sulci location between specimens of the same species is becoming a larger issue (page 105). The recent introduction of the MRI and fMRI appears to be the realization of a new volumetric environment to which they are referring.

The Talairach system is proportional and orthogonal (although they discuss it using the term parallelograms instead of rectangles). They establish a horizontal reference plane containing a line between the commissura anterior, CA, and the commissura posterior, CP. Although this line appears skewed from the horizontal of the eyes, it does form a dividing line between the thalamus and the Pretectum, and the Superior Colliculus of the midbrain. They erect two perpendiculars to this line and divide the distance between these perpendiculars into three equal distances. The gross distances related to this grid are used to normalize the brain coordinates.

The time is rife for the creation of a new mapping system based on measurements by a modern coordinate measuring machine and the “morphing” capabilities available on the PC computer. The use of a modern coordinate measuring machine with six degrees of freedom would give results far better than that of the simple stereotaxis machines of the biological literature (such as that of Ffytche, Guy & Zeki based on the machine of Horsely & Clark (1908). Combined with a modern digital computer, these capabilities would allow a coordinate system to be created that would be scalable to the brain of a given individual as he/she grows and also be scalable between individuals. By using a sufficiently fine “wire frame” initially, the resulting map would also be scalable to any degree of fineness required as research moves forward. Because of the variability of the location of fissures on the mature brain, it would be recommended that the specific brain used as the model be named. Although the brains of the higher primates are not spherical, the techniques of modern cartography provide a wide range of projections from which to select one optimal for displaying a brain.\textsuperscript{116} A number of interrupted

equal area projections appear promising. Because of the lack of symmetry in the sulci, it would be useful to provide a map of both hemispheres of at least one brain so the differences could be placed in perspective for the reader.

Ffytche, Guy & Zeki\textsuperscript{117} have made a preliminary step in this direction. However, they did not use a sufficiently powerful mesh approach, relied on information gained from a series of slices in one plane of a brain, and employed an electrical simulation involving a mathematical approximation of 25 terms. They estimated that the 25 term expansion was within 5% of the actual value represented by a potential on a homogeneous sphere. They then noted there was a closed form solution for this situation. They offered no reason for their use of an approximation instead of the actual equation. See previous discussion of the map provided by Tootell, et. al.

**15.1.7.1.2 Translation and correlation of notations relative to vision**

Brodmann never documented the significance of his numbering system relative to the surface organization of the brain. Bailey and von Bonin noted that: “It is strange that for many years the scientific world has accepted statements, and built upon them, for which no direct proof had ever been given\textsuperscript{118}.

This work will attempt to observe the notation of Brodmann while also indicating the V(n) notation when appropriate. Zeki\textsuperscript{119} has emphasized the difficulties of being specific in this area. He noted that his “provisional areas 18 & 19” were not strictly the same as Brodmann’s areas 18 & 19. He also noted that the designations OA and OB, used by von Bonin and Bailey in 1947, were not truly synonymous with areas 18 and 19 of Brodmann either. He also noted the statement of Lashley & Clark that: “areas 18 and 19 of Brodmann could not be told apart and that, together with the area 7, they should be considered a single functional area.” Finally he noted that von Bonin, et. al\textsuperscript{120}, defined an area 18 that was much larger than area 18 of Brodmann.

The V(n) notation is difficult to track in the literature because of its continuing expansion and perfection with respect to locations on the cortex. Zeki has provided one of the few figures attempting to show the location of the V(n) areas, through V(6), on a two dimensional projection of the cortex of *macaque*\textsuperscript{121}.

Leigh & Zee have recently provided considerable material that relates the notation of various authors and can be used to prepare a composite view of the topology and topography of the visual portions of the brain\textsuperscript{122}.

**15.1.7.2 Coordinates perpendicular to the plane of the cortex surface**

A similar problem arises with the cross-section of the cortex. It is generally described in terms of six layers of finite thickness beginning at the outside. They are each generally heterogeneous. Even Noback had difficulty naming them and gave two designations for each layer (three for the 6th). They are:

1. **Plexiform**, or **molecular layer**
2. **External granular layer**, or layers of small pyramidal cells.
3. Layer of medium-sized and large pyramidal cells, or **external pyramidal layer**

4. Internal granular layer, or layer of small stellate and pyramidal cells
5. Inner, or deep layer of large pyramidal cells and
6. Spindle cell layer or layers of fusiform cells, or multiform layer.

More recently, Nolte\textsuperscript{123} settled on a subset of Noback’s labels as indicated by the bold labels in the above set. For the fifth layer, he settled on a different variant, the Internal pyramidal layer. Nolte also provides a correlation between the images of the cross section of the neocortex obtained using a variety of different stains.

15.1.7.3 Correlation of retinal topography to the cortex

Early studies focused on the occipital cortex discovered coarse correlation between the surface of the cortex and the retina. As the precision of measurement became better, it was found the correlation became poorer, particularly with respect to the foveola. Through extensive experimentation involving lesions at different locations in the visual pathways, it was discovered that the foveola was not represented in the primary visual cortex at all. This has caused consternation for a long time. The reason why a topographical representation of the foveola does not appear in V1 of the primary visual cortex will be presented below. In recent years, it has been found that the topographical correlation between the retina and the LGN and rest of the cerebral cortex decreases with path distance from the retina, essentially disappearing in areas V4 and beyond. It is now relatively clear that the LGN requires a strict correlation with the topography of the two retinas in order to accommodate stereopsis. It is also clear that area V1 requires reasonable topographic correlation with the retina, although in the context of a larger field than the instantaneous field of the eyes, in order to sense and begin the response to threats to the animal. Figure 29.3 of Zeki\textsuperscript{124} clearly shows the failure of the transposition of the map of the retina found in the LGN to the primary visual cortex in anything resembling a conformal or an equal area pattern. Beyond, or starting with, V4 the signal manipulation within the cortex need not concern itself with a high degree of spatial correlation with the retina or the exterior world. The signal manipulation becomes abstract. It involves a spatial field of view that is much wider than the instantaneous field of the eye and is carried out in the context of an earth oriented inertial system. This is obviously necessary to accommodate inputs from the aural and somatosensory systems.

Because of the limitations of morphology in determining the functional purpose of a structure, the limited sensitivity of electrophysiological instrumentation to detect the illumination of a single photoreceptor, and the predominant use of degeneration techniques in the study of the brain in the laboratory, the precision with which a given area, of less than a millimeter square, of the cortex can be related to the visual field imaged on the retina is quite limited. [too long]

15.1.7.3.1 Precision of correlation of retinal and striate areas

While good maps of the projection of the retinal surface onto the lateral geniculate nucleus are available\textsuperscript{125}, very little data is available correlating precisely the area of the retina to that of the various areas of the cortex in human. Most of the data is from lower chordates and only relates field angles in object space to lineal dimensions in various areas of the cortex. Because of the large size of the illuminating source, the results are generally crude. Montero, et. al\textsuperscript{126} have provided data for the albino rat. Using a 2\textdegree diameter source, they attempted to map object space to the cortex using the vascular pattern overlaying the cortex as a reference. They state that: “The primary visual area presented a distinct and precisely arranged retinoptic organization.” However, their measurements do not support such a sweeping statement to the level desired in this work. Their receptive fields (RF) were typically 10-20\textdegree in area 17 with more space dedicated to the less peripheral areas of

\begin{itemize}
\item Montero, V. Rojas, A. & Torrealba, F. (1973) retinoptic organization of striate and peristriate visual cortex in the albino rat. Brain Res. vol. 53, pp. 197-201
\end{itemize}
the retina. No mention was made of the fovea or foveola. This would be expected with a 2° diameter source. RF’s in the 40-60° range were obtained in the lateral (18a) and antero-medial (anterior part of 18) peristriate cortices. These are large areas of overlap for adjacent 2° stimuli and the results can hardly be considered a “map” in the common vernacular.

15.1.7.3.2 Inferential correlation of retinal and striate areas

The experimental limitations described above have led to the heavy use of inference to trace the signal paths of the visual system. As an example of the use of inference, Zeki inferred from the work of Guld & Bertulis\(^\text{127}\) that the intersection of the vertical and horizontal meridians of the visual field as traced on area 17 should define the projection of the foveola on the cortex. However, Guld & Bertulis did not report measurements within a 0.9° radius of the putative center of the foveola (they only used the word fovea) and they stressed that their measurements involved “averaged gross responses.” They also omitted any specification of the size of the fovea in this small monkey (total weight of these animals was less than twice the weight of the human brain alone) nor did they specify the focal length of the eye. They did provide a magnification factor relating a distance on the cortex to a an angular distance in object space as a function of object space angle. Zeki used the term foveola in the title to a paper based on his inference. He did not make any measurements related to the actual point of fixation of the retina to the assumed area of the striated cortex. Using degenerate techniques, he reported some consternation when the destruction of an area within 2° of the presumed point of fixation as mapped to the striated cortex did not result in any subsequent degeneration in his area V4\(^\text{128}\). He notes in the following paragraphs that his area V4 also receives inputs from V2 and the pulvinar areas. In an earlier paper\(^\text{129}\), Zeki had presented a map of the cortex that gave a distinctly different perimeter for the “macular” than in the 1978 paper. This perimeter only barely encompassed the putative intersections of the horizontal and vertical meridians. Most of this perimeter laid anterior to area 19. No specification as to the perimeter, or the center, of the smaller foveola was given. He reported consternation when he found his data did not support his assumption that the foveola was at the intersection presumed. In fact, the data does not even support a specification of the larger retinal area defined as the fovea.

15.1.7.3.3 Correlations resulting from fMRI experiments

Figure 15.1.7-4 provides a redrawn version of Heide using the Brodmann notation as transcribed by Demarest\(^\text{130}\). The annotation describing the lateral surface, except as noted, given by Heide is:

- AC–Anterior cingulate cortex On medial surface
- FEF–Frontal eye field
- IPL–Inferior parietal lobule
- IPS–Intraparietal sulcus
- MPP–Medial posterior parietal region, extending into the precuneus.
- PFC–Prefrontal cortex
- PMC–Premotor cortex
- P.Ci.–Posterior cingulate cortex On medial surface
- PPC–Posterior parietal cortex
- SMA–Supplementary motor area On medial surface


SPL—Superior parietal lobule

This view does not highlight the importance of the inferior gyrus of the temporal lobe in vision\(^{131}\). It appears that areas 21 and 37 participate in the correlation of audio and visual sensations.

All of these areas were found to contribute to the production of memory guided saccades by fMRI. Generally, the participation was bilateral based on an evaluation of oxygen consumption.

![Figure 15.1.7-4 Annotated lateral profile of the human brain showing areas supporting the visual function observed through fMRI experiments involving memory guided saccades. See text for notation.]

### 15.1.8 The hydraulics and pharmacology of the brain

Because of the high density of neurons within the brain, it is much easier to study the hydraulics and metabolism of the neurons within the brain than at remote sites in the PNS. This section appears here for that reason. Otherwise, it would be located in Section 10.8. Some of the more detailed aspects of metabolism do appear in Section 8.6.

The pharmacology of the brain, like that of the PNS, has been studied from an early day based on the assumption that the signaling function of neurons is entirely chemically based. As noted by Finlay & Zigmond, “Chemical techniques were first applied to the study of the nervous system in a systematic way in the late 19th Century.” They were writing in a massive tome of over 163 individual, and frequently short, chapters by a variety of authors. This official publication of the American College of Neuropsychopharmacology includes only the briefest discussion of the functional characteristics of the neuron, and essentially nothing on its electrophysiology. Chapter 5, Electrophysiology is limited to brief discussions of action potential generating neurons and a variety of voltage and current clamping techniques used to examine the electrical signals found by

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probing the interior of the neuron. The book contains virtually no equations or detailed chemical reactions in its 2000 pages. Finlay & Zigmond also refer to the battle during the middle of the 20th Century over whether neurons were primarily electronic or chemical in fundamental nature. They indicate “it had become clear that the great majority of the information transfer between neurons involved chemical signals, even in the brain, . . .”

While Bloom lists a hierarchal series of levels used in research in the neurosciences, the absence of any consideration of the semiconductor physics of the neuron is striking. His position (in the earliest page of the official bible of the neuropsychopharmacology community) is that the entire field of neuroscience is focused on the chemical activity associated with the space between the pre- and post synaptic surfaces.

This work does not accept the assertions contained within the above two paragraphs and explains why. The results of this new framework far outstrip those found in the literature based on the above concepts. A major simplification is the demonstration of the electron as the primary carrier of signaling information (neurotransmitter) within and between neurons. Such a simplification eliminates the complex (and to date unexplained) process frequently labeled signal transduction between neurons. This putative process involves the release of chemicals (exocytosis) in response to an electrical signal traveling down the axon, their transport across the gap junction and the subsequent regeneration of an electrical signal following their ingestion (pinocytosis) by the post synaptic membrane. Both exocytosis and pinocytosis would presumably involve the formation of vesicles containing the desired neurotransmitters. Richelson struggles with the signal transduction mechanism. The discussion becomes ever more complex as it proceeds.

A minor problem appears to focus on the definition of the forebrain (and its clear separation from the frontal lobe of the cerebral cortex). Bloom describes the forebrain as consisting of the cerebral cortex, thalamus and hypothalamus. Nolte and others would suggest the cerebrum as a label encompassing this group (and other elements of the CNS). Placing the thalamus exclusively in the cerebrum group appears to denigrate many of its other important (but generally not cognitive) functions.

This section will expand the nomenclature used in the pharmacology of the brain to provide additional conceptual flexibility. Such flexibility is necessary to present a comprehensive and cohesive model of the operation of the brain. This expansion shows that most of the data in the literature remains useful but in a slightly different context. As in the retina, conventional hydraulics plays a major role in the operation of the brain.

In the biological system, the vascular system is much more dynamic, and elastic, than previously realized. Buxton has recently demonstrated how this dynamic character has significant effects in the short term operation of the brain. He has shown that the transient electrophysiological responses measured with NMR and fMRI techniques depends greatly on the flexibility of the venous elements of the vascular system within a given voxel of the brain. These variations appear to be both species and location (within the brain) dependent.

15.1.8.1 The conventional Neurotransmitter dogma of pharmacology

The determination by the neuroscience community (primarily the pharmacology branch) that synaptic signaling was a chemically dominated process was followed by the elucidation of a “neurotransmitter dogma.” While the contents of this dogma are difficult to locate in precise form, Snyder & Dawson have offered their variant. Their physical interpretation of the dogma says neurotransmitters:

1. are stored in synaptic vesicles which release their contents by exocytosis involving fusion with the plasma

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membrane and expulsion.

2. diffuse to closely adjacent cells, where they interact reversibly with membrane protein receptors which influence cellular events through the mediation of intracellular second messenger molecules or by influencing ion permeation.

McCormick provides a different variant based on time and functionality. His definition of a neurotransmitter is:

1. It causes post synaptic responses that are both quick in onset (e.g., <1 msec) and relatively short in duration (e.g., <tens of milliseconds).

Under these interpretations of the neurotransmitter dogma, nearly any neuro-active chemical becomes a neurotransmitter. Currently, the literature boasts over a dozen so-called neurotransmitters. They are all described as acting individually between the pre and post synaptic membranes, and apparently in parallel. This situation leads to the interesting question of how any particular neurotransmitter could have a significant effect in the presence of so many other independent neurotransmitters? It also leads to an absurdly complex synaptic junction. The example in Shepherd makes this point.

Meanwhile the electrophysiology branch of the neurosciences has proceeded to explore the synapse as an electrical circuit element. It has largely ignored the idea of a neurotransmitter dogma. This dogma appears to be archaic.

15.1.8.2 First order hydraulic plan of the brain

Figure 15.1.8-1 provides a gross baseline for discussing the hydraulics and pharmacology of the brain. The neuron shown is a hybrid derived from the diagrams of Section 10.8.1 for purposes of discussion. It exhibits the input structure typical of a horizontal cell and the output structure of a typical ganglion cell. Ganglion cells with differential inputs have been discussed in the literature. However, no major group of such cells has been identified. The output structure of the hybrid shown consists of one unmyelinated axon section and two myelinated sections (interaxons). The unmyelinated section contains the hillock. The sections are separated by Nodes of Ranvier. These Nodes contain active electrolytic devices, Activa, identical to that between the dendrite and the axon within the bulk of the neuron. The nucleus of the neuron is shown as a white circle for completeness. It plays no active role in the signaling operation. The neuron is shown imbedded in a capillary bed. When many neurons are in close proximity, they are frequently described as surrounded by a similar inter-neuron matrix. This matrix, or capillary bed, frequently includes glia closely associated with one or more neurons. Within the CNS, these glia are known as astrocytes. Outside of the CNS, they are named Schwann cells.

The intricate physical arrangement between the neurons and the glia has made it difficult to define the precise role of the glia. The conventional morphological view is that they provide the myelin wrapping associated with the interaxons. A more recent view based on metabolism is that they provide supplementary lactate to the portions of the neuron remote from the glycolysis manufacturing function. This explanation would help explain the limited chemical flow along the length of the neuron both internal to and external to the electrical conduit.

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portion of the axon/interaxon. It would also help explain the estimate of ten astrocytes to every neuron within the brain by Tsacopoulos & Pellerin139. A more interesting ratio, in the context of the next figure, would be between the number of astrocytes and the number of Nodes of Ranvier.

The overall cellular arrangement is separated from the arteriole and venoule by the blood-brain-barrier as shown. This conceptual barrier is very important in the operation of the brain. However, it is not a free-standing structure. It appears to be formed by the distinctly different composition of the arteriole walls compared to the walls of peripheral arteriole.

Figure 15.1.8-1 The first-order hydraulic plan of the brain.

Figure 15.1.8-2 provides a more detailed description of the static hydraulic situation. Highlighted within both the soma of the neuron and the glia (astrocyte) is the mechanism supporting the glycolysis of glycogen received from the arteriole via the capillary bed. Highlighted within the axon and interaxon shown are the areas supporting the manufacture of glutamate via the tri-carboxylic-acid (Krebs) cycle. The variant of the TCA cycle described here is based on the glutamate shunt discussed in Section 8.6. Three area labeled TCA appear in the figure. They are subscripted for purposes of discussion. A premise shared with Magistretti & Pellerin is that the demands for glutamate, and its reclamation, are high in the neuron140. Magistretti has suggested that the glia support the neurons by manufacturing significant amounts of lactate that can be easily transferred to the neural cell by diffusion (their lactate shuttle hypothesis). The remainder of the Magistretti & Pellerin vision of neural metabolism and neuro-transmission is not adopted in this work.

Both this and the previous figure are compatible with neurons generating both analog (electrotonic) and phasic (action potential) output signals. Note there is no mechanism for transferring large molecules such as sodium or potassium through the plasmalemma of the conduits of a neuron. Charge transfer is by electrons moving through the electrical diode formed by the asymmetrical bilayer structure of the lemma (Section xxx). In this work, the only method of signal transmission between conduits of the neural system (dendrite to axon and axon to dendrite—or interaxon) is via electron flow through Activa (Section xxx). The area of minimal spacing between such conduits is shown by the solid black rectangles. These area invariably contain a liquid crystal of hydronium

that exhibits negligible ability to support diffusion of large molecules between conduits Section 10.8.xxx).

For areas of conduit near the soma of the neuron, the TCA cycle receives pyruvate from the glycolysis generator in the soma. This pyruvate is used to manufacture glutamate. The glutamate is converted into GABA and CO2 in an electrostenolytic process on the surface of the conduit that releases an electron into the conduit (Section xxx). If preferred, the process can be considered to release a hydrogen ion into the inter-neuron matrix. The result is the same from an electrical perspective. A net increase in charge between the surfaces of the plasmalemma is generated. This creates a voltage. This is the primary source of electrical potential found between the various plasmas of the neuron and its surrounding matrix.

![Figure 15.1.8-2 A more detailed hydraulic environment of the brain.](image)

For Nodes of Ranvier distant from the soma of the neuron, it would be of considerable benefit if glutamate could be manufactured more locally. It is reasonable to adopt the Magistretti proposal that the glia manufacture lactate (chemically similar to pyruvate) near these sites by glycolysis (labeled Gly2 in the figure). This requires that the peripheral portions of the neuron only convert this lactate into glutamate in support of the neurons operation. Sites performing this manufacturing are labeled TCA2 and TCA3. Although not described in the figure, there is also a simpler mechanism to re-manufacture glutamate from GABA within the confines of the conduits (Section 7.7).

The dashed arrows highlight a major function associated with the capillary bed. This is the removal of waste products associated with the various manufacturing steps and the electrostenolytic process powering the neurons.
This function will be discussed more fully below.

15.1.8.2.1 Global hydraulic plan of the brain

Chapter

15.1.8.3 Major chemical equations of neural metabolism

The above figures bring the major chemical events and equations related to neural metabolism into better focus. The primary mechanism powering the neurons is the electrostenolytic process. It involves the conversion of glutamate into GABA. It is glutamate that is the primary neuro-facilitator of biological neurons. It is GABA that is the major reaction product of electrostenolysis. The availability of glutamate and the removal of GABA are the primary controlling factors in the operation of the neural system.

Many authors speak in terms of the complete oxidative reduction of glucose when speaking about neuron operation. The steps in the complete process of reducing glucose to water and CO$_2$ are shown in Figure 15.1.8-3. This figure is exceedingly complex. However, it is dwarfed by the complexity of the operation of the tri-carboxylic acid (TCA) cycle explored by the nutrition community$^{141}$. While it shows the consumption of energy in considerable detail, it does not illustrate the vast number of enzymes and cofactors considered necessary to complete these processes. The figure can be divided into three major functions. The first is the production of pyruvate or lactate from glucose or glycogen. This overall process is called glycolysis and it occupies the left half of the figure. The process is generally associated with the nucleus of a cell. The upper right portion of the figure centers on the tri-carboxylic-acid (Krebs) cycle. This cycle is responsible for the creation of many precursors to other chemicals used in the organism. Most of these are not involved in neural signaling. However, the glutamate shunt is of particular importance in neural signaling. It is the source of the electrical potential used to power the Activas within and between neurons. This glutamate shunt is described in detail in Section 8.6. The operation of the tri-carboxylic-acid cycle is generally associated with the mitochondria of the cell. The lower right of the figure is generally associated with the ribosomes of the cell. It is the area of protein formation and is associated with the ultimate oxidation of the myriad of residue molecules from this process.

The nominal operation of any neuron depends on the nominal operation of all of the manufacturing steps shown in the above figure. Such operation requires the presence of nominal amounts of the reactants and the resulting reaction byproducts. *This requirement in turn requires the nominal rate of supply and removal of all of the involved products.* The availability, reaction, and removal of all of these products are key to the homeostasis of the organism. Section 8.6.3 presents the homeostatic concentration of several of the critical metabolic element derived from glucose (glycogen).

As indicated above, providing power to the neurons for signaling purposes is centered on the glutamate shunt shown on the right of the figure. This shunt draws upon $\alpha$-ketoglutarate from the TCA. This material is aminated to form glutamate. Following amination, the glutamate can participate in an electrostenolytic process on specialized asymmetrical regions of the lemma of neurons. In this stereospecific process, the glutamate is decarboxylated to GABA. The process releases an electron on the inside of the lemma. Multiples of such electrons are the source of electrical potential between the inside and outside of the lemma. It is this electrostenolytic electron pump that is the realization of the ion-pump conceptualized by Hodgkin & Huxley in 1952.

The glutamate shunt occupies a very limited section of the TCA cycle. It only releases a few units of ATP in order to achieve a potential across the substrate membrane of about 154 mV. Hence a single operation of the

electrostenolysis process at the molecular level does not account for the complete oxidation of any glucose. However, repeated operation of the TCA cycle via the glutamate shunt will consume all of the energy equivalent to the oxidation of a complete molecule of glucose. Similarly, the operation of multiple electrostenolytic sites simultaneously will consume ATP at a rate that can be related back to the complete oxidation of multiple glucose molecules within the same time period.
Figure 15.1.8-3 An end-to-end description of the oxidation of glucose. The figure can be divided into three portions. The left portion represents the glycolysis of glucose or glycogen to pyruvate or lactate. The upper right represents one variant of the tri-carboxylic-acid (Krebs) cycle. It includes the glutamate shunt so critical to the operation of the neural system. The lower right represents the oxidative phosphorylation of the residues from the earlier chemical operations. Modified from Magistretti, et. al., 1995.
As defined here, the following equations summarize the steps involved in the operation of providing power to each neuron in the neural system.

Supply of glycogen by diffusion  
\[ \text{Eq. 15.1.8-1} \]

Glycogen \( \rightarrow \) pyruvate (aerobic conditions)  
\[ \text{Eq. 15.1.8-2a} \]

Glycogen \( \rightarrow \) lactate (anaerobic conditions)  
\[ \text{Eq. 15.1.8-2b} \]

Lactate \( \rightarrow \) pyruvate (as required)  
\[ \text{Eq. 15.1.8-3} \]

Pyruvate \( \rightarrow \) \( \alpha \)-ketoglutarate (TCA)  
\[ \text{Eq. 15.1.8-4} \]

\( \alpha \)-ketoglutarate \( \rightarrow \) glutamate (glutamate shunt)  
\[ \text{Eq. 15.1.8-5} \]

Glutamate \( \rightarrow \) GABA + CO\(_2\) (electrostenolysis)  
\[ \text{Eq. 15.1.8-6} \]

GABA \( \rightarrow \) glutamate (transamination)  
\[ \text{Eq. 15.1.8-7} \]

GABA removal by diffusion (alternate)  
\[ \text{Eq. 15.1.8-8} \]

Many of the above steps generate CO\(_2\) as a byproduct (Section 7.7.3). This material must also be removed, primarily by diffusion back to the blood stream.

15.1.8.4 The stereo-chemistry of many neuro-active materials

Figure 15.1.8-4 describes the stereo-chemistry of several important neuro-active materials. The top row is designed to show the similarity of the two polar nutritionally non-essential amino acids, aspartic acid and glutamic acid. It also shows the result of the electrostenolysis process. By the removal of one CO\(_2\), glutamic acid produces the reaction product, GABA. These three amino materials all exhibit a terminal carboxylic group.

The lower row shows two materials capable of interfering with the electrostenolysis process through the ability of their carboxylic group to occupy the stereo-specific electrostenolysis site but not complete the electrostenolysis process.

15.1.8.5 Redefinition of neurotransmitters and neuro-facilitators

Within the context described above, it is appropriate to re-examine the descriptive labels of various materials involved in the above operations. Previously, it has been common to describe any material that appeared to stimulate neural activity as a neurotransmitter. Any material that tended to suppress neural activity was labeled a neuro-inhibitor. While the term neurotransmitter is firmly embedded in the literature at all levels, it does not provide a broad enough framework for research.
purposes and it is misleading. This work adopts a broader framework based on how the subject chemical impacts the operation of the glutamate shunt. Materials participating in the stereo-specific electrostenolytic process directly are described as either primary neuro-facilitators or primary neuro-inhibitors depending on whether they drive the reaction to the right or to the left. There are only two materials that can drive the equation to the right, the stereo-specific primary neuro-facilitator, glutamate, and the secondary neuro-facilitator, aspartate. There is only one material known to drive the equation to the left. That is the stereo-specific primary neuro-inhibitor, GABA. Glycine is in a separate class because of its combination of stereo-specificity and its lack of a second carboxyl group. It is able to occupy the site designed for glutamate at the electrostenolytic reaction site. However, its monocarboxylic character leaves it unable to release CO₂ and generate the required free electron. Therefore, its presence tends to stop the electrostenolytic process at a particular molecular level site. Other examples will be discussed below.

The resulting framework is summarized in the column of TABLE 15.1.8-1 labeled “New designation.” The framework recognizes the electron as the only true neurotransmitter and a series of materials as neuro-facilitators and neuro-inhibitors. The neuro-facilitators can be further divided into primary and secondary classes depending on whether they participate directly in the above equations or act only as necessary enzymes or cofactors. The secondary neuro-facilitators and neuro-inhibitors can be divided into two classes. Class 1 materials directly affect the site of the electrostenolytic process. Class 2 materials affect the ability of other chemicals to reach (or be removed from) those sites. This framework leads to a much simpler interpretation of the pharmacological results from varying the concentration of one or more of the above materials. TABLE 15.1.8-1 can be compared with a similar listing by McCormick in Shepherd⁴².

### TABLE 15.1.8-1
Framework for materials impacting neural operation

<table>
<thead>
<tr>
<th>Theory</th>
<th>Chemical</th>
<th>Electrolytic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Material</td>
<td>Historical designation</td>
<td>New designation</td>
</tr>
<tr>
<td>electron</td>
<td>~</td>
<td>Neurotransmitter</td>
</tr>
<tr>
<td>glutamate</td>
<td>Neurotransmitter</td>
<td>Primary neuro-facilitator</td>
</tr>
<tr>
<td>GABA</td>
<td>Neurotransmitter (frequently)</td>
<td>Primary neuro-inhibitor</td>
</tr>
<tr>
<td>Aspartate</td>
<td></td>
<td>Alternate primary neuro-facilitator</td>
</tr>
<tr>
<td>L-Dopa</td>
<td></td>
<td>Class 1 neuro-facilitator</td>
</tr>
<tr>
<td>Glycine</td>
<td></td>
<td>Class 1 neuro-inhibitor</td>
</tr>
<tr>
<td>Dopamine</td>
<td>Neurotransmitter</td>
<td>Class 1 neuro-inhibitor</td>
</tr>
<tr>
<td>Acetylcholine</td>
<td>Neurotransmitter</td>
<td>Neuro-inhibitor</td>
</tr>
<tr>
<td>Histamine</td>
<td>Neurotransmitter</td>
<td>Neuro-inhibitor</td>
</tr>
<tr>
<td>Norepinephrine</td>
<td>Neurotransmitter</td>
<td>Neuro-inhibitor</td>
</tr>
<tr>
<td>Serotonin</td>
<td>Neurotransmitter</td>
<td>Neuro-inhibitor</td>
</tr>
</tbody>
</table>

Serotonin is 5-hydroxytryptamine. L-Dopa can participate in electrostenolysis. Dopamine cannot. L-Dopa can be considered a “sticky” neuro-facilitator. Its reaction product may not leave the site promptly. Vasopressor is synonymous with vasoconstrictor.

A discussion by Paul is closely aligned with the idea of a primary neuro-facilitator and a primary neuro-inhibitor. He says: “Pharmacological studies utilizing drugs which selectively block or augment the actions of GABA or glutamate support the notion that these two neurotransmitters, by virtue of their often opposing excitatory and inhibitory actions, control, to a large degree, the overall excitability of the CNS.” The terms neuro-facilitator and neuro-inhibitor can be inserted into this sentence in place of the term two neurotransmitters with excellent results. His subsequent discussions of GABA and glycine as neuro-inhibitors does not recognize their fundamentally different chemistry and resultant roles.

McCormick follows the conventional wisdom in separating neuro-active substances into two categories. The first consists of the neurotransmitters, substances that result in rapid post-synaptic response and have a short term impact. The second consists of the neuro-modulators, substances that have a longer lasting duration in their impact on the neural system. McCormick notes that the distinction between these two categories is not always easy. He attempts to relate their action to a variety of receptors within the synaptic gap. However, he only presents a textual discussion. No organization of these materials (labeled neuro-inhibitors here) is offered.

Dowling has constructed a different description of neuro-active materials based on his view of their relevant chemical properties. He has provided examples more closely aligned with this work. He describes neurotransmitters as acetylcholine and a variety of amino acids (L-glutamate, L-aspartate, GABA and glycine). He describes neuromodulators as monoamines and peptides.

This work takes a different view than that of McCormick and proposes a more detailed and specific set of neuro-inhibitor categories than Dowling. Class 1 neuro-inhibitors interfere with the direct chemical reactions outlined above. Class 2 neuro-inhibitors interfere with the enzymatic actions required in support of these actions. Class 3 neuro-inhibitors include those materials changing the diffusion parameters of the interneuron matrix (or the walls of the vascular channels. Class 4 neuro-inhibitors interfere with the electrical conductivity of the interneuron matrix. Referring to the above discussion of Paul, glycine (a mono carboxylic amino acid) is a class 1 neuro-inhibitor because it occupies the position of glutamate in the electrostenolytic process. By occupying this position, to the exclusion of glutamate, it inhibits the glutamate-GABA electrostenolytic process.

Close examination of the stereochemistry of the neurotransmitters according to Dowling in the context of the electrostenolytic process quickly divides the his neurotransmitters into the classes defined above. Glycine becomes a class 1 neuro-inhibitor because it occupies a site in the electrostenolytic process designed for glutamate. GABA becomes a primary neuro-inhibitor because it pushes the fundamental electrostenolytic process to the left. L-glutamate becomes a primary neuro-facilitator and L-aspartate becomes an alternate primary neuro-facilitators.

The following summarizes the proposed framework. The framework applies to all neurons, including those generating both tonic and phasic output signals. The designation neurotransmitter (when referring to the transmission of a signal between conduits of a neural system) should be reserved for the electron. The

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designation primary neuro-facilitator is reserved for glutamate. It is one of only two dicarboxylic amino acids that can participate in the electrostrenolytic reaction of neurology. The designation primary neuro-inhibitor is reserved for GABA. It is the main reactant of the electrostrenolytic reaction. The presence of excess GABA slows the normal electrostrenolytic reaction. That tends to lower the electrical potential of the conduits of the neurons. The result can be positive or negative depending on the location of the change in potential. Aspartate acts as a backup for glutamate under certain conditions. It and glutamate are the only two amino acids with charged polar groups (due to their two carboxylic acid groups). It is able to perform in the electrostrenolytic process but the reaction product, β-amino propionic acid, is not able to be recycled via the glutamate shunt. It must take a more circuitous route through the TCA to regenerate glutamate. Glycine is a simpler amino acid than aspartate and contains only one carboxylic group. It is a class 1 neuro-inhibitor because it can occupy the electrostrenolytic site using its one carboxylic ligand but cannot release carbon dioxide to form GABA. Thus, it cannot complete the process and provide a free electron to the neuron conduit. Many other chemicals can interfere with the homoeostatic conditions supporting the electrostrenolytic process (at least a dozen according to McCormick). They are all neuro-inhibitors. A possible exception would be a material that could accelerate the clearance of GABA from the electrostrenolytic site. Chemicals that cause constriction of the blood vessels, or otherwise inhibit the diffusion of glycogen to the neurons or CO₂ from the neurons can be considered neuro-inhibitors. Any material, such as monosodium glutamate that can raise the concentration of the dicarboxyl acid, glutamate, in the area of the electrostrenolytic process can be considered a secondary neuro-facilitator.

There is no requirement for any of the above materials to diffuse into or through the less than 100 nm wide gap junctions involved in neuron-signaling. While it is easy to draw caricatures showing such diffusion, it is difficult to implement the caricatures. This very small region is filled with a hydronium liquid crystal (Section 10.8.xxx) that discourages diffusion.

15.1.8.5.1 The putative role of glutamic acid decarboxylase

Paul discusses the very early (1950) studies of the role of GABA in neural activity. He described the role of an enzyme called glutamic acid decarboxylase (GAD) in the brain of mouse. It was closely associated with a cofactor, pyridoxal 5’-phosphate (PLP). It is not clear whether GAD was actually isolated or only postulated during these studies. It is quite possible that GAD was postulated to act as the substrate actually provided by the cell membrane in electrostrenolysis. Alternately, it is possible that both GAD and PLP are required as part of the electrostrenolysis process.

15.1.8.5.2 The putative role of dopamine

Dopamine is not found within the brain in significant amounts. Bannon, et. al. estimate “dopamine-containing neurons constitute less than 1 in every 10⁵ – 10⁶ neurons in the mammalian brain.” However, its medicinal importance is great in controlling neural diseases. The stereo-structure of dopamine suggests that it can occupy the stereo-specific site at the electrostrenolytic process designed for glutamate. As a result, dopamine can act as a class 1 neuro-inhibitor just as glycine can.

15.2 The block diagrams, schematics and circuits of perception

There is a major difficulty in discussing the signal pathways of the visual system in the cortex because of the profusion of overlapping names applied by various authors in the recent literature. Even the venerable lateral geniculate nucleus is called the lateral geniculate body in many works. The problem is getting worse as more detailed knowledge is accumulating concerning the brain. Within the next few years, it will be absolutely mandatory that a new and more detailed reference map of the brain be prepared. It will probably be computer

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generated based on a wire frame model that can be morphed to apply to any human brain regardless of size. With that model in hand, it will be possible to adopt a universal set of labels that will be scalable (downward) as more detailed knowledge is gained. For now, it will be necessary to give alternate names in parentheses at frequent intervals in the following discussion.

15.2.1 Fundamental differences in the signal paths of the phyla

The lower the animal in the phyla, the less signal processing carried out within the retina and brain. Euglena employs zero signal processing. The signal from the photoreceptor cell passes directly to muscle tissue. At the highest end, the signal processing is significantly impacted by the degrees of freedom between the eye and the body. To achieve two degrees of freedom and a large angular extent, the signal processing in Chordata has incorporated projection neurons to allow a much higher level of encoding of optical signals and the associated reduction in the size of the optic nerve. The effective incorporation of projection neurons has required a redistribution of the signal processing neurons within the visual system. In Mollusca, there is no signal processing within the retina. It is all located within the initial structure of the optic lobe. In Chordata, there is very significant signal processing within the retina in addition to the spatial encoding of the ganglion cells of the projection system. The bipolar and lateral cells associated with the initial processing of spatial, chromatic, shape, and polarization (if appropriate) information have been located within the retina rather than within the optic lobe as in Mollusca. In the configuration of Chordata, the ganglion cells of the retina and the decoding cells of the optic lobes appear to be unique to the visual systems of that phylum. These are the cells that employ action potentials for signal transmission. The lack of these cells and action potentials in Mollusca is strong support for the position that the visual system is primarily an analog based system. Projection neurons, and action potentials, are employed primarily to support signal transmission over distances large compared to a few millimeters.

With the above conclusion in mind, the Neural Doctrine expressed by Barlow\textsuperscript{146} in 1972 provides some material worthy of consideration (except for his first dogma) when discussing perception. Elimination of the first dogma also implies a reduction in acceptability of the ideas related to probabilistic events and “trigger events.” An exploration of the capabilities of signal thresholding will be found to be more useful. Young\textsuperscript{147} has also provided some early but relevant material. Kabrisky\textsuperscript{148} stresses the analog nature of the signal processing within a neuron and has summarized a variety of concepts. Hubel\textsuperscript{149} has provided some more recent material and recent references. Spillmann & Werner\textsuperscript{150} have edited a large volume on visual perception, with references. However, the same caveats concerning action potentials and triggering apply to all of these works. The neural system is an analog based system. Only the projection neurons (found primarily if not exclusively in Chordata) develop and utilize action potentials. The significance of the analog nature of the signal manipulation function will be seen to have an extraordinary impact on the time required to process information within the cortex.

It appears that all of the sensory information is processed by an animal in a consistent geometric perspective to aid in threat determination. However, in the higher animals, an additional (and to a large extent parallel) level of processing is associated with detailed threat evaluation and the analyses of abstract forms. This level is not organized topographically with respect to the retina or the spatial surround of the animal. This dual context will be defined more completely in section 15.X (2). In Chordata, this processing is clearly more complex than in Arthropoda and at least most of Mollusca.

\textsuperscript{147}Young, J. (1964) A model of the brain. London: Oxford University Press.
As has been mentioned several times, the signals generated in the retina are currents but the signal processing occurring in the retina is based on the summation of voltages. This is the case for both the luminance and chrominance information. The voltages involved are exponentially related to the original currents. Some of these voltages have been inverted to provide a negation function. The question arises as to whether the signal ultimately perceived by the brain is still directly proportional to a current, or is it a voltage equal to the current times a diode impedance function. This question plays a critical role in the derivation of the spectral response of the eye and may also play a key role in the chromatic response of the eye; it will be discussed further in Section 15.6 (in PART II of Chapter 15).

15.2.1.1 Architecture of Mollusca

The visual circuit configuration of the mollusc, *Octopus vulgaris*, provides a unique starting point, at the circuit diagram level, for the discussion of perception using the same precise definition of perception. Figure 15.2.1-1 from Young, provides a typical circuit configuration shared, except for the addition of the projection neurons, with *Chordata*. In the case of Chordata, the neural circuitry of the plexiform zone (labeled *plex.* in the figure) would be transferred to the retina and the projection neurons would be introduced between that layer (known as the plexiform layer in *Chordata*) and the remainder of the optic lobe(s). The initial portion of the projection system, the ganglion layer would appear as it does in the chordate retina and the decoding portion would appear in place of the plexiform zone in the initial regions of the optic lobe(s). The complete nomenclature of Young is shown on page 661-669 of that work.

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15.2.1.2 Architecture of Chordata and man

There have been many models of the visual architecture of Chordata proposed during the last 50 years. There have been more than a dozen in the last twenty years. However, these models generally reflect a parochial view and attempt to explain all vision in terms of various two channel systems. The difficulty in that approach is shown in a table by Bridgeman. It lists six recent attempts where each investigator provides two names to define distinct pathways within the system. However, no two investigators, out of the six, agree on the name of even one of the two pathways. Frequently, the investigators do not differentiate between the volition mode of operation from the autonomous mode. By defining a more comprehensive model, it is possible to relate the various portions studied by the above investigators to a broader whole.

The basic premise of much of the literature is that the topological organization of the brains of all chordates is fundamentally the same. A second premise is that the topological organization is well correlated with the topographic features of the chordate brain. In recent work, differences in topological features of a few millimeters compared to the nominal topographic location have been described for individual within a species.

Rosenquist has provided a review, many caricatures and a tabular description of the interconnections within the visual system of cat (without considering the forebrain or much of the midbrain) based primarily on elementary traffic analysis supported by anatomy. The lack of attention to the accessory optic nucleus in his discussion is a particular problem. This feature is labeled the Precision Optical System (POS) within this work to suggest its actual importance. His figure 4 will be addressed more completely below.

The most obvious morphological change within the phylum is the significant growth in size and complexity of the cerebral cortex as one moves up the phylum toward the most sophisticated members of chordata, the great apes. Less well recognized is the similar growth in the size of the pulvinar and other elements within the thalamus.

15.2.1.2.1 Fundamental differences in the visual signal paths within Chordata

There are significant variations in the signal processing and importance of different signal paths among members of Chordata. One of these variations is based on a tradeoff between rotational ability of the eye and the need to “track” objects in the scene. As discussed earlier, Anthropoidea have a remarkably spherical ocular compared to other species in the phylum. This leads to an excellent capability to rotate the line of fixation using only the muscles of the eye. Most of the lower animals in the phylum do not share this capability. They are only able to rotate the eye through a few degrees. The freedom of the eyeball relative to the head is primarily to support the tremor needed to support imaging of the scene. These animals have a stronger need to track an object within the field of view without relying on rotation of the eye relative to the head. Otherwise, they, must rely on rotation of the head or the entire body to track an object. This latter approach is often seen in birds. Frogs have little flexibility between their eyes and head and between their head and body. They appear to rely almost entirely on signal processing within the retina to track moving objects. These animals, as well as many grazing animals appear to have a highly developed 2nd lateral matrix, populated by various cell classes including the amercine cells, within their retina. Man, on the other hand exhibits only a minimal population of neurons in the 2nd lateral processing matrix.

The above tradeoff appears to lead to much less spatial processing in the retina of man than is found in the lower

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chordates. This makes extrapolation of the signal processing data acquired from the lower chordates to man very dangerous.

Probably the most important variation among the chordates is in the degree of complexity that has evolved in order to introduce the analytical channel of vision. That of the primates appears to be the most highly evolved, however some information puts the birds and possibly many other species, close behind. This evolutionary feature involves the foveola of the retina, the PGN/pulvinar couple, the cerebellum of the midbrain and the Pulvinar pathway in an entirely separate signaling path from the conventional retina, LGN, visual cortex pathway. The analytical pathway involves a totally different signal processing architecture than that of the awareness pathway. This is clearly demonstrated by Plate 2 in Davson based on an earlier presentation of Stiles\textsuperscript{154}. This plate shows the significant difference in the color matching performance of the human eye as a function of location within the field of view. It defines the “Maxwell spot,” a feature that appears to correlate with the foveola and also with many after image effects discussed in this work. [Figure 15.6.5-3] provides a dashed box surrounding the areas of the old brain listed above. The development of the elements within the box can be directly related to the position of the animal within the phylogenic tree. They are most highly developed in man. It will be shown that many of the most important visual functions do not involve area 17 of the cerebral cortex (the so-called primary visual cortex).

15.2.2 The Information flow in perception and cognition

The visual system is now understood well enough to begin moving into the questions of cognition as it relates to the frontal lobe of the cerebral cortex, and consciousness in general. Prior to moving in this direction, it is absolutely critical that all terms be defined clearly and precisely. Normally, this level of definition is not found within the neuroscience community when discussing these subjects. The word awareness is a particular problem. It is proposed that the saliency map forms a unique location (boundary) within the neurological system. It separates the operations of the sensory systems which provide information to the saliency map and the higher level operations of the brain which access this data. The sensory systems provide the interpretation and perception of the raw input and derive the abstract (vectorized) signals placed in the saliency map. The higher level cognitive centers use this map to cognate on the environmental situation described by the saliency map and to prepare instructions to be implemented by the efferent neural systems.

In the above context, a subject can achieve perceptual awareness without achieving cognitive awareness. The former relates to the operation of the system prior to the saliency map and includes the performance of the “zombie.” It also includes the performance of many subjects exhibiting “blindsight.” These subjects are able to perceive and respond to threats and other visual symbology without being cognitively aware of the threat or symbology.

There is another point of clarification related to the efferent signal paths of vision. It may be useful to consider the output of the higher cognitive centers as being passed to an equivalent of the saliency map before implementation. This equivalent may be directly related to what is frequently called the premotor areas (as differentiated from the motor areas) of the brain. This delineation would aid in separating those subjects who have cognitive awareness of an event but cannot report that awareness using the conventional methods (primarily speech). Such cases are becoming better known as the techniques of psychophysical evaluation become more sophisticated. Even ordinary subjects are frequently tongue-tied during moments of anxiety (even though they may point at something fervently or take other protective action).

The above comments can be focussed by considering the original series of Frankenstein movies. In the original movie, Frankenstein was a true zombie. He could perceive his surrounding, take reflexive actions and respond to commands (after the second act). However, he could not cognate on what he perceived, nor prepare responses based on his own volition. It

was only in subsequent movies that amour was used to lead Frankenstein to attempt cognition and eventually develop the “I want” phenomenon that lead to his implementation of the volition mode of operation.

It is important to understand both the topology and the temporal aspects of information flow within the visual system if the operation of the system is to be appreciated in detail. Although the topology has been addressed widely in the literature, little if any attention has been paid to the temporal aspects associated with the signal paths. The importance of the temporal aspects of these signal paths will become more obvious in this section and will be addressed in more detail in Sections 15.2.5 through 15.6.5.

Treisman\textsuperscript{155} presented a conceptual discussion of the cognition process. She discussed the cognition process, as it relates to vision, in terms of a series of maps connected by simple transforms. In the process, she introduced the term, “saliency map” to describe the mechanism that encodes for the relationship between different features in the image or otherwise relates information stored at different locations in the cortex. Recent major strides in nuclear particle and magnetic resonance imaging of the body have provided significant new information in how the perceptual and cognitive processes are accomplished. This imagery, when combined with psychophysical excitation have shown that different features of a given sensation are frequently, if not always, extracted, and possibly stored, at different discreet regions or zones of the brain. These results can be interpreted as the brain storing different individual vectors (engrams), related to individual features of the excitation, at different locations. If true, there must be a mechanism for assembling these individual vectors into group as part of the ultimate cognitive process. The total number of significant vectors need not all be vision related.

Magnetic resonance imaging, at its current level of resolution is a magnificent new tool. Its sensitivity is quite remarkable. However, its current practical resolution limit of about 0.5 mm is severely limiting in vision research. There may be as many as one-half million neurons (each containing at least one Activa) in a volume bounded by 0.5 mm (roughly the number of active devices in the brain of a local telephone switchboard computer). Science is still extremely limited in its ability to probe the cortex.

It is suggested that the subject can be better understood if the ideas of Treisman are placed in a broader context. Figure 15.2.2-1 defines a master saliency database that is all-encompassing. It is shown as a flat file as usual but may represent a hierarchal database. It contains all of the information available to an organism from instantaneous inputs as well as memory. The dimensions of the database (spreadsheet) are in abstract space and it may consist of more dimensions than can be easily presented on paper. Part of this abstract space includes spatial coordinates. These spatial coordinates appear to be related to inertial space and have little to do with the finite instantaneous field of view of the eyes. This inertial space may be interpreted from the perspective of the animal’s body, or of its head in those animals exhibiting significant flexibility between the head and body. The important aspect is that, it is not directly related to a visual field of view. The conceptual and graphical style of the figure appears similar to that provided by Fuster\textsuperscript{156}.

The eye is not a camera, it is fundamentally a change detector (that is highly pointable in the human case). The data acquired from the eye can be filtered and the relevant information stored in the proper assigned areas of the total database much as a computer stores new data within its overall disk space. The total saliency database (spreadsheet) includes overall vectors that include components from the feature extraction engines located at different sites in the brain. These overall vectors may contain the relevant data or may only consist of addresses for the location of the specific data (tags) stored at the feature extraction sites that receive data from all of the sensory channels. Kandel, et. al. use the term “labeled line code” to define a concept similar to that developed

\textsuperscript{155} Treisman, A. (1986) Features and objects in visual processing \textit{Scientific American} vol 255(5) pp 114-125

here\textsuperscript{157}. McClurkin, et. al. appear to have adopted a similar concept\textsuperscript{158}. Their report is based on a combination of information theory and conventional pattern psychophysics. They do introduce the important concept of separable code segments (vectors). This concept provides a much shorter code to describe each complete scene element. This is the approach used in the figure.

Figure 15.2.2-1 Steps in the cognitive process highlighting the Saliency Database (or spreadsheet). The overall process of cognition can draw on all of the perceptual mechanisms shown. See text.

Some of the obvious feature extraction mechanisms are grouped in the figure for convenience of presentation. If the database only includes addresses, the relevant vectorial data stored in specific zones can be accumulated by the "current engine" that is tasked with accepting current information from the sensory systems. Other vectorial data can be simultaneously accumulated from the long term memory of the organism via the "recall engine."
The long term memory database may be subdivided into segments of complete vectors (or segments of complete vector addresses). The vector or address segments may correspond to the feature extraction engines shown in the lower part of the figure or they may not. If they do, the question remains as to whether the long term memory occupies different space than the short term memory. It may be that all memory is located in the individual feature extraction zones of the cortex. The most likely architecture of memory probably follows the architecture of current day large scale computer databases.

In a follow-on paper and lecture, Treisman expanded their concept in a manner that is not accepted here. They show the area dedicated to color feature processing as separable into three individual color maps of red, yellow and blue. According to this theory, by the time the data reaches the brain it has been encoded into one channel of luminance, the R-channel, and two channels of color difference, the P- and Q-channels. There does not appear to be any reason for the information carried by these channels to be decoded back to their original constituents.

The attention of the highest cognitive processes can be focused on specific zones of the database. This data can either be copied into a short term memory separate from or contained within this highest cognitive process.

When collecting information in real time, the “current engine” assimilates information vectors that include much more information than suggested in the figure of Treisman. The overall vector associated with every event contains at least a time tag and a master orientation tag (no claim is made as to understanding how these tags are organized). Other tags would be “null values” unless relevant information was received through a specific sensory channel. In the case of an event such as the explosion of a firecracker at close range, many of the sensory channels may respond. In the figure, the visual, aural and some of the somatosensory channels are shown responding. It is likely that the olfactory sensory system may also respond. Following feature extraction at the extraction sites, a very complex vector is created in the Saliency database shown by the crosshatched area. It is accompanied by many other vectors not directly related to the Event but consisting of background information. This information may be considered context information by the highest cognitive processes and is also shown in the saliency database of the figure.

The concept of a single vector containing individual vectorial components can be compared to the discussion in Zeki & Ffytche of subject G.Y. and the Riddoch syndrome. In the case of G.Y., major damage to V1 has left the subject “blind” in one hemifield with regard to spatial detail (except for macular sparing), color and some degree of motion. However, he is able to sense motion, some degree of orientation, and possibly other features in the spatially blind hemifield.

Zeki, et. al. have published a similar paper concerning subject PB. PB exhibits virtually no visual form discrimination capability as a result of brain ischemia from a severe electrical shock. However, when presented a series of color panels of essentially equal luminance, he can accurately name the colors presented to his visual field but cannot describe the shape of the panels.

This ability to sense features in a scene without being able to perceive the spatial geometry, of

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160Features and objects: The fourteenth Bartlett memorial lecture
that scene has called into review the entire concept of blindness as well as the difference between visual discrimination and awareness. The above papers take care to tease these concepts apart and provide more detailed definitions of the situations encountered. Gnosopia (from *gnosis* = knowledge and *opsia* = vision) is subdivided into a series of terms that can be correlated with the idea of a single, multi-component, saliency vector associated with an event.

The extraction mechanism shown are only meant to be illustrative. It is not necessarily true that the labels shown are realistic. In the auditory area for example, it is not known whether the mechanisms used are based on the frequency domain or the temporal domain. Although the duration of a signal is clearly important, it is not clear whether it is adequate to record the number and amplitude of the harmonics associated with the pitch of a tone or whether the relative phase of the individual harmonics is also important.

The database should not be considered a map of vision space, or of aural space. It is entirely abstract. The database need not have a variable “granularity” to accommodate the variable resolution of the fovea versus the surrounding area of the retina. Once the features are extracted and associated with a time tag, the question of spatial resolution of the visual field becomes moot.

Marr, working in the area of computational vision (not computer vision) as a sub-area of cognition has presented a number of fundamental ideas that appear consistent with the above discussion. He defines vision as a process that produces from images of the external world a description that is useful to the viewer and not cluttered with irrelevant information. The primary purpose of vision is the building of a description of the shapes and positions of things from images.

He distinguishes between three levels of understanding about vision: the level of computational theory, the level of representation and algorithms, and the level of processing device or hardware implementation. He begins with the position that the functional term process is very broad. To understand complex information processing systems, he employs a lower level concept of a representation. “A representation is a formal system for making explicit certain entities or types of information, together with a specification of how the system does this.” He then defines the result of using a representation to describe a given entity a description of the entity in that representation (emphasis added). He goes further and defines an algorithm as a description of a transformation between two representations. Thus his representation combines the saliency vector and the rules used by the engines to create it. An algorithm may apply to the operation of several engines used to derive a given representation.

Marr provides a simplified model of the stages of vision focused on various representations. He begins with the retinal image and progresses to a primal sketch that can be more or less related to the representations in either the LGN or V1. This is a sketch with some degree of spatial fidelity to the original retinal image but defined in terms of symbols such as edges, bars, blobs, etc. He then moves to what he defines as a 2.5D sketch and then a 3D sketch. These representations are less and less spatially oriented. He defines the 2.5D sketch as a representation of properties of the visible surfaces, such as orientation, in a viewer centered coordinate system. The 3D sketch is object-centered rather than viewer-centered depiction of the three-dimensional structure and organization of the viewed shape along with some level of description of its surface properties. In this work, his object-centered view is considered an earth oriented inertial centered view to accommodate the input from other sensors and his 3D representation is entirely vectorial and abstract.

Although not addressing the cognitive area in this work, it is clear that there are other engines associated with command generation. In the present context command generation includes two sub elements, command assimilation and command implementation. Command implementation involves the actual creation of the neuro-
motor signals delivered to the peripheral nervous system (including the oculomotor system). The command assimilation element is more complex and need not be accomplished in only one engine. The command assimilation engines can be considered a mirror image, although not necessarily a 1:1 image at the detailed level, of the feature extraction engine architecture.

Our understanding of the flow of information within the visual system is currently undergoing rapid change. This subject will be addressed in detail in the following sections.

15.2.2.1 Time delays (latencies) in signal transmission

The community has suffered from the poor definition of the time delays associated with vision. The term latency has been applied to a broader range of time intervals than is appropriate. The On-line Medical Dictionary defines the term as “the time between onset of a stimulus and peak of the ensuing action potential.” This definition is inadequate for several reasons. First, a term is needed to cover tonic waveforms as well. Second, a term is needed applicable to the same point in the stimulus waveform and the response waveform. Third, a term is needed that clearly applies to the result of a series of mechanisms. A superior concept is to use the explicit term time delay to mean the difference in time between a feature of a stimulus and a feature of the observed response. With this definition, adjectives can be added to satisfy specific situations.

There is a second problem when discussing these time delays. The community has focused on differences in the velocity of axon signal transport without regard to the distance to be traveled. As discussed in Section 15.2.5.3.1, timing within the visual system is significantly impacted by the signal path lengths. The primary purpose of Meyer’s loop, in both its simplest and expanded descriptions, is to provide a variable time delay between different areas of the retinal image.

Before the 1989, the morphologists studying the brain did not consider the time delays between a stimulus and the responses at different locations within the cortex. This has recently changed and been a major cause of the change in understanding introduced by Zeki. He found that the signals arriving in his area V5 frequently did so before an approximately equivalent signal arrived in area V1. This situation was clearly in conflict with the hierarchal concept of the visual system within the brain. Since that time, several major contributions to this subject have appeared164. The Zeki school may still not have adopted the star network as the basic organization of the brain but this will come to pass as more data is collected and the concept of parallelism in the architecture of the brain fades from the literature.

It is recommended that latency be restricted to its more common use in biology and psychophysics. There it is used to indicate the time between the stimulus and the response of an animal at a very crude level of precision.

15.2.2.2 Labeling information flow

The literature contains a wide range of very simple diagrams describing the flow of information from the retina to the cognitive elements of the brain. Most appear to exist to support introductory pedagogy. Fuster has frequently used a “ladder” diagram illustrating the flow of signals within the brain in hierarchal form165. It is an extension of the conceptual figure in Section 11.1.4 and has remained unchanged since 1980. Unfortunately, all pathways are shown generically and bidirectional. A more specific diagram would recognize the unitary direction associated with the signal paths outside of the CNS and the starlike pattern of connections within the CNS. Even within the CNS, most signal paths are unidirectional. Another problem with his diagram is the lack of parallel paths related to the analytical and awareness modes of visual signal processing. No provision is made for the alarm mode of signal projection. His extension of the hierarchy to include polymodal association of signals and signal

processing engines is a useful conceptual extension of the diagrams in Section 15.2.3. To be compatible with this work, the terms polymodal and unimodal are best changed to polysensory and unisensory. This allows each sensory channel to possess multiple internal operating modes without a semantic conflict.

Recent authors in neuroscience have defined two modes of vision. The labels on-line system and seeing system being the most frequently found. Here again, the more detailed models of this work allow these terms to be interpreted more precisely. In Crick & Koch, they define the seeing system as related to consciousness while the on-line system is not. They relate the on-line system to more speedy action. Using the model of this work, the seeing system combines the cognitive mode of operation following deposition of abstract signals into the saliency map, with the awareness and analytical modes that provided those depositions. Their definition of the on-line system is more compatible with the operation of the POS in response to alarm mode signals. Responses generated within these modes and mechanisms frequently occur before the appropriate data is forwarded to the saliency map. The time delays associated with the POS are much shorter than those related to the analytical pathway (Section 15.2.2.6). Thus, such responsive actions occur before “seeing” can occur.

The use of the terms afferent and efferent have been very helpful in the peripheral neural system. However, it appears to break down when discussing the complete visual system. There is a need for a third category. It appears that the terminology evolving in computer systems may be preferable. In that context, sensory signal flow up to the old brain control point (the TRN of the diencephalon) would be considered afferent. Control signal flow from the old brain (diencephalon and superior colliculus) to the peripheral system would be considered efferent. All other neurological activity within the brain would be considered cognitive and command signal flow.

Using this notation, afferent signal paths will be considered those transmitting signals toward the cognitive mechanisms in stage 5. Conversely, efferent signal paths lead away from stage 5. Within stage 4 and stage 5, the system is not organized in a hierarchal structure. Some signal paths are internal (in a broad use of the word). For these signal paths, the term association neurons or neural paths remains appropriate. Because of the size of many of the feature extraction engines, it is frequently necessary to use association neurons within the engine. When proceeding between engines without a clear destination, the term X-Y association neurons can be used where X defines the originating location and Y the terminating location of the neuron. For those association neurons passing through the corpus callosum, the designation commissural neuron can still be used but the X-Y prefix is still useful. The designation -fugal to indicate neurons traveling away from an engine and -petal to indicate neurons traveling toward an engine appear acceptable but less specific than the dual notation prefix.

15.2.2.3 Developing the concept of attention

xxx Define two distinct levels of attention (autonomous and conscious)

Describe the (type of automatic neural system) nominal precision optical system

Bandwidth of attention channels may not be the same as the earlier channels in the overall system
The characteristic bands of hearing illustrate this feature.

Recent progress in the neurosciences has led to ever greater discussions of the subject of attention. However, the entire subject remains at a conceptual level. As Van der Heijden somewhat cynically noted, “The term ‘attention’ is very often used and nearly as often misused in the experimental psychology literature. In general, it seems that the unwritten rule is that, where an explanation in terms of whatever explicit mechanism is not readily

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conceivable, it makes good science to invoke the concept attention to do the job.”

Up to now, this phenomenon has always been discussed with respect to consciousness. However, this is an arbitrary limitation. While it is not yet possible to describe the phenomenon of attention in any detail, it is possible to differentiate the concept into attention at the subconscious (autonomous) level and attention at the conscious level. This separation is introduced because it is quite obvious that the precision optical system is able to make decisions concerning which elements of a scene presented to it are of major importance and to concentrate its activity with respect to those elements. In many cases, the POS concentrates its attention and makes decisions as much as a few milliseconds before the central cortex has even been notified of the event. In making its decisions, the POS determines which elements of the scene will be brought into the line of fixation and therefore which scene elements will be presented to the analytical system for further analysis.

15.2.2.3 Ontogenesis of the visual system EXPAND or CONSOLIDATE

See Sections 2.2.4 & 2.2.5. See Hamilton.

15.2.2.4 Cortico-cortico connections and principle pathways

Several authors have attempted to provide global maps of the interconnections within the brain of human and ape168. At the present time, such a presentation is too complex to be useful except for traffic analysis and it is changing almost daily based on new analyses. The complexity of the task requires a multi-dimensional tabular approach (a database) listing the source and destination of major nerve fiber (bundle) and a pathway label if available. The physical length of the pathway is also important in studying timing issues. Such a tabulation could be keyed to the top level schematics of the next section. Goodale & Milner have provided a valuable discussion of traffic analysis based primarily on psychophysical evidence resulting from lesions of the brain169. As a result, this paper assumes direct connection between areas of the cerebral cortex without the option of relay via the TRN. Nolte has provided a variety of individual tabulation of parts of these paths. He points out the difficulty of the task; the corpus callosum interconnecting the two hemispheres of the human brain contains over 300 million axons170. Blinkov & Glezer have provided a tabulation of the properties of the human corpus callosum171. Berlucchi has described the roles of different regions of the corpus callosum172.

15.2.2.4.1 The corpus callosum and the anterior and posterior optical radiations

A unique feature of the visual system that may also be found in auditory sensor channels is the fanning of the individual neurons between each LGN and area 17. This feature is clearly involved in controlling the degree of synchronism between the data carried by the different neural channels. Although not normally recognized, there is a second fanning of many of the related neural channels within the retina. This fanning is due to the single point of exit for all ganglion neurons. It forces the different signal paths to encounter different signal delays on route to the thalamus. This fanning is named Reyem’s loop (palindromic to Meyer’s loop) in this work. The variation in timing among these different channels is of tremendous importance in vision as discussed below.

15.2.2.4.2 The pulvinar radiations

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Berlucchi, G. (2004) Some effects of cortical and callosal damage on conscious and unconscious processing of visual information and other sensory inputs Prog Brain Res vol 144, pp 79-93
This work has chosen to describe the signal paths between the PGN/pulvinar couple and Area 7 of the parietal lobes as the pulvinar pathway for purposes of semantic continuity. However, there is no reference in the literature to any fanning of the neural paths within this radiation, a la Meyer’s loops. Based on this model, none would be expected. All of the ganglion cells originating the signals traveling over these paths originate in a very small area of the retina. It is expected that all of the signals traveling over these paths would exhibit essentially the same delay prior to arrival at the PGN. Similarly, all of the signals passing over the pulvinar pathway would be expected to exhibit the same delay.

15.2.3 Signaling at the circuit level in the brain

Recording electrical waveforms, both in-vivo and in-vitro has recently become an area of active research. Markram and his team have been particularly active and have provided extensive bibliographies. However, there are serious problems with the conclusions being drawn due to the conceptual model being assumed. The material generally assumes the signals within the higher order engines of the cortex are processed in serial streams. The assumption is also made that the neurons are two terminal circuits. On the other hand, the investigators do recognize that the number of signal inputs to a typical neuron number in the hundreds. Because of the inadequate circuit models available, most investigators have relied upon phenomenological based analyses to ascertain the mechanisms generating the observed signals. The studies have led to the use of multiple probe recording methods but have not led to rigorous control of the in-situ input signals. In some cases, it appears that electrotonic neurons have been forced into phasic mode through the injection of charge into one electrolytic cavity or another of the specimen.

While the use of multiprobe techniques is mandatory if a full description of a neural circuit is to be obtained, it is equally mandatory that the DC potentials associated with these signals be recorded. The operation of a neuron is critically dependent on the difference in potential between the emitter (dendritic) and base (poditic) terminals of the Activa contained within the neuron. This potential must be known to an accuracy of 1-2 mV to be definitive.

A large problem is the frequent use of neural simulators based on a set of differential equations developed on phenomenological grounds and limited to the action potentials related to stage 3 signaling neurons. The procedure is reminiscent of the kinematic models historically used in studying the photoexcitation process of vision. These simulators do not recognize the three terminal characteristic of the typical neuron. While these simulators may be of pedagogical value at the undergraduate level, they cannot be depended upon to provide a relevant description of the performance of a typical neuron at the research level.

Another problem is the frequent reliance upon statistical methods to estimate the performance of deterministic circuits. As shown in Chapters 8, 9 & 10, except at the quantum-mechanical level, the performance of neurons and synapses are entirely deterministic. The response may be statistical if the input signal is statistical or if there are uncontrolled inputs impacting the overall experiment (a problem that vexed Huxley & Hodgkin in the early days and may have impacted Markram, et. al. in 1997).

Some of the labels placed on morphological elements of individual neurons appear inconsistent with the larger neurological literature (Fig 1 of Markram, Lubke, et. al. 1997).

It is important to recognize that the stage 4 (high level signal processing) circuits of the cortex (those within a particular engine) are predominantly electrotonic and operate as part of an asynchronous computer. The circuits are asynchronous because they do not rely upon a central clock. However, they are synchronous in the sense that adjacent neurons may process individual bits of a parallel word, received from an earlier circuit complex, in temporal parallelism. Forcing neurons within these engines to oscillate through the injection of charge into their soma or axon must be considered a pathological situation. McGeer, Eccles & McGeer show how this is accomplished with recordings of the soma potential at better than one millivolt precision\(^{176}\). While the technique may be useful in traffic analysis, the data obtained related to the performance of nearby neurons is necessarily suspect.

Within most engines of the cortex, there is no requirement for action potentials to be generated. Signal processing can occur with signal levels of only a few millivolts amplitude. The minimum amplitude criteria is met when either memory cells can be activated or action potentials can be generated by ganglion cells associated with stage 3. This level is known to be only a few millivolts for action potential generation by a ganglion cell.

For the foreseeable future, it will be very difficult to determine the signals exciting a specific electrotonic neuron, or complex of neurons except under two conditions. First, if the entire neuron or complex of neurons are teased out of a particular engine without rupturing any of the dendritic, poditic and axonal tissue. Second, the entire engine is isolated and the paths of all input signals from stage 3 (signal transmission) circuits are accounted for and controlled. In these two cases, it becomes possible to control the input signals to the circuit(s) of interest. Under other conditions, the best that can be said is that a signal was introduced (in the presence of other unknown and uncontrolled signals) and a particular response was observed.

\[\text{xxx see comments regarding Konig, et. al. in Section 14.6.1 Move part or all here}\]

**15.2.3.1 Brief review of the electrolytic topology of the neuron**

To aid the reader, a selection of figures from other Chapters of this work have been assembled here. They summarize the operational aspects of the fundamental neuron and synapse between two neurons.

**Figure 15.2.3-1** repeats [Figure 10.6.1-2]. It shows the three distinct regions of the typical neuron (based on a pyramid cell for convenience). By probing the soma of this cell, the investigator may contact the dendroplasm, frequently making up the bulk of a soma, the podaplasm, shown on the right and extending into contact with the Activa Base, or the axoplasm (not labeled but extending from the axon into the soma in the area of the hillock).

The DC potentials within the soma (particularly within the extended volume of the dendroplasm)
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vary significantly with location as documented in Figure 15.2.3-2 that is reproduced from [Figure 10.6.1-3]. While it may not be necessary to record the potentials immediately adjacent to the Activa, providing the DC potential as well as the AC waveform is important in interpreting the action of the neuron.

Figure 15.2.3-2 The variation in DC potential throughout a typical electrotonic neuron under quiescent conditions. Note the large variation in the potential of both the dendritic and poditic plasmas. The minute Activa is found in a thin region of the darkened area between the areas labeled dendrites and axon, and below the label Podite. Modified from Guyton, 1976

Figure 15.2.3-3 repeats [Figure 9.2.2-4] showing the basic cytological and electrolytic circuit diagrams associated with a typical neuron. The cytological features introducing additional circuit elements into the complete electrolytic circuit are not shown (see Chapters 8 & 9). While the synapses are shown in the cytological diagram, they are treated as simple transfer impedances in the circuit diagram. The various lemmas are shown as diodes shunted by a capacitance in the region of the synapses. Along the rest of their periphery, they constitute nearly perfect insulators (still exhibiting significant capacitance). The physical arrangement of the lemmas form active devices (Activas) at their junctures. These three-terminal devices, conceptually labeled synapses are critically dependent on the electrical potential between the presynaptic axon, the post synaptic neurite and the interneural plasma. When properly biased (as normal in-situ), the synapse demonstrates the electrical properties of a high quality diode (Section 9.4). They pass electrical charges orthodromically (from within one axon to within one neurite) with very high efficiency. Under some circumstances, they do represent a significant resistive impedance. Their electrical properties are entirely deterministic since the number of charges involved in even the smallest signal detectable by the Activa is far above the quantum-statistical range. Synapses normally operate in the electrotonic mode, even when transferring signals known as action potentials. However, they can be, and have been observed to oscillate under pathological bias conditions instituted by man. A hybrid closely related to the synapse, the Node of Ranvier acts as a monopulse oscillator under normal bias conditions (Section 9.3).

As shown in the referenced chapters, the electronic performance of the neurons, based on the Activa, are completely analogous to man-made transistor circuits. All of the circuit analysis tools found in conventional analysis and design of electronic circuits can be used in the study of biological (electrolytic) circuits. The
relatively low charge transit velocity of electrolytic circuits does require treating some of the circuits as if the contain discrete delay lines.

**Figure 15.2.3-3** Cytological caricature and electrolytic schematic of a typical lateral cell (horizontal or amercine in retina; pyramid in cortex). See Section 9.2.2 for details.

15.2.3.2 The need to isolate and identify specific circuit elements
As shown in Chapters 8 & 9, the electrical performance of a neuron is completely controlled by the Activas within it and the associated circuit elements and biases applied to it.

### 15.2.3.2.1 Frequent ambiguity of the EPSP

Many authors discuss an excitatory post synaptic potential (EPSP) based on probing the soma of a neuron. They generally do not determine whether it is the dendroplasm or the podaplasim that was accessed by the probe. This situation can cause considerable confusion with regard to the observed waveforms. While the signal obtained from the dendroplasm may only contain a small component associated with the axon potential (AP) of the post synaptic neuron, the signal obtained from the podaplasim will generally exhibit the sum of the signals applied to the dendritic terminal plus the generated in the axoplasm. In the stage 3 encoders (commonly described as ganglion cells in the retina but frequently labeled interneurons in cortical research), the poditic waveform includes both an electrotonic input component and a pulse output component due to the generation of an action potential by the neuron. The waveform from the “soma: of the “interneuron” in figure 2(B) of Markram, Wang & Tsodyks is of this type.

There is a clear need to differentiate between an ESPS associated with a dendrite and those associated with a podite. The two forms of the ESPS are of opposite polarity but have the same impact on the subsequent axoplasm. A positive going dendritic signal is compatible with the designation ESPS in an oscillatory circuit. However, a positive going poditic signal is inhibitory with respect to the production of an action potential.

### 15.2.4 Neural encoding within the cortex

At the base level, Sperling, et. al. have shown that the luminance signals transmitted over the stage 3 circuits of the visual system are decoded linearly by the stellate cells. As a result, the signals are presented to the brain in the same form as they appeared before encoding by the ganglion cells of the retina.

As in the low level signals associated with the optic nerve and optic radiation, the rest of the cortex employs commissure consisting of multiple individual neural paths (small commissure) to transmit complex signals. These small commissure are known as nerves in anatomy. However, the use of nerve to indicate a group of individual neural paths is awkward in the present context. In the low level signals, these small commissure transmit temporally coherent signals derived primarily from spatially coherent imagery related to only a portion of the complete field of view. In the case of the higher level signals associated with the cortex, these small commissure transmit complex information that is not spatially coherent with respect to object space. These small commissure employ multiple bit signals constituting one “word.” The individual “words” are sent serially. In the vernacular, these words are transmitted as asynchronous bit-parallel word-serial signals. To record a complete word associated with perception requires multiprobe signal capture and more knowledge of the intrinsic machine language used in the cortex than is currently available. In this case, the multiprobe technique refers to the use of multiple probes within a single signal processing engine. The asynchronous operation of the cortex can lead to a variety of misinterpretations that are widely exploited in magic and can be a major source of vertigo and other unsettling feelings.

The book by Tasker, et. al. is one of the few that have addressed neural coding. More recently Steriade, et. al. have provided detailed analog waveforms that contribute to our knowledge of neural coding. These works will be reviewed in Section 15.5.2.5. They both show what little knowledge is available concerning the machine
language used within the cortex. The discussion in tasker is particularly clear in highlighting the inadequacy of attempts to use single point excitation to elicit high level perceptual responses. Even in the most recent exploratory efforts to provide rudimentary sight for the blind, the signals introduced as stimuli do not conform to natural signals. These stimuli do not emulate real signals in intensity or coding. As a result, the neural system treats them as interference rather than emulations of real signals. Pulse type interference introduced into the non-cortical portion of the visual system is usually perceived as achromatic flashes of points of light. Stimuli introduced into the cortical portion is more likely to be perceived as a more abstract feature, and occasionally be associated with a color. In the aural system, a stimulus at any frequency tends to be perceived as a low pitched sound below 300 Hz. In other sensory channels, the perception is frequently of a paraesthetic character. Tactile perceptions have not been reported. Tasker, et. al. recognized their inability to communicate with the organism using the brain’s “modality code.”

15.2.5 RECENT ARCHITECTURE (Top level topology and schematics) of humans, ca ’98

Until recently, the architecture of the brain, particularly with respect to vision has been determined by its gross morphology based on dissection and trauma. With the recent advances in tracer techniques, using dyes and radioactive nucelotides, great progress has been made in determining the terminal points of individual neurons within large commissure. The results have been enlightening and frequently surprising. They strongly suggest a new architecture for the higher level signal processing within visual system. This “emerging architecture” (ca. 2002) will be discussed in Section 15.6.5 following a short review of the recent proposed architecture (ca. 1998). While the ca. 1998 model is more advanced than the texts published through 1998, it remains largely compatible with it. The ca. 2002 model begins to diverge significantly and the divergence is so significant that it relies upon the ca.1998 model to provide the reader a feeling of continuity.

Carpenter & Sutin have taken a strong position that “All sensory impulses, with the sole exception of the olfactory ones, terminate in the gray masses of the thalamus. from which they are projected to specific cortical areas by the thalmocortical radiations.” They go on to describe the role of the thalamus; “In terms of physiological functions the thalamus and related neuronal subsystems are concerned with high fidelity transmission of sensory information , with input selection, output tuning, synchronization and de-synchronization of cortical activity, parallel processing of information and signal storing and modification.”(giving their internal reference of 2077) These are the very functions that are further detailed below.

The Guillery school has expanded significantly on the base of Carpenter & Sutin by introducing the previously ignored thalamic reticular nucleus, TRN. This structure intercepts virtually all neural paths involving the thalamus. A significant question arises as to whether the interception involves a termination of the individual axons, involving a serial synapse along a given neural path, or merely a collateral axon leading to a terminating synapse within the TRN.

It will be noted again below but it is important to stress;

The visual systems of man begins to diverge significantly from the lower primates and other species in the area of the pulvinar, the thalamic reticular nucleus (TRN) and the so-called perigeniculate nucleus (PGN) or region of the thalamic reticular nucleus. One cannot discuss the visual performance of man (particularly with regard to reading and the analysis of fine detail) based on the writings applicable to these areas in lower animals.

This section will present several figures describing the architecture of the visual system essentially as presented
in the literature up through 1980, except for an additional emphasis on the perigeniculate nucleus, PGN, in its role related to the foveola. It is the PGN/pulvinar couple, specific parts of the diencephalon, that has been shown to be critically important in the unique capabilities of the human visual system. This discussion of the recently defined architecture will be followed by another section focused on the findings documented during the last twenty years that have not previously been correlated into a composite presentation. These findings further perfect and document the architecture and operation of the visual system in the region between the retina and the higher cognitive centers of the cerebral cortex.

15.2.5.1 Profile view of the visual topology of human and other primates, ca. ‘98

Figure 15.2.5-1 shows a more detailed profile view of the topology of vision than found in the current literature. It extends the figure of Snider\(^{181}\) reproduced in Torrey. The figure is also compatible with Humphrey\(^{182}\), as reproduced in Ottoson (1983). Perry & Cowey have noted (with stated surprise) that 10% of the nerves within the optic nerve of monkey proceed to the PGN (an area of the thalamus) rather than to the LGN\(^{183}\). These nerves were described as both \(\alpha\) & \(\beta\) cells, of the type previously believed to only present in the LGN. Vanegas has also documented the direct connection of unspecified areas of the thalamus to areas 7 and 8 of the cortex\(^{184}\). The figure heightens the awareness of the diencephalon as a gatekeeper for signals traveling to and from other elements of the brain. This subject will be explored further in Section 15.6.5. This figure draws attention to a secondary chiasm (or bifurcation) found, at least, in the higher chordates. It stresses the great importance of the PGN and other elements of the diencephalon to the overall visual process in humans. The importance of the circuits associated with the PGN are critical to the visual system in many chordates, essentially any animal with a highly developed fovea(s). The presence of a fovea suggests the animal is able to employ muscular tremor to perform a higher degree of data extraction in this limited region of the retina. The functional importance of these channels can be recognized immediately from the figure in Section 2.6.1 by Ganong and also reproduced in Kandel, et. al. without attribution. The highly important information associated with the fovea is not transmitted to area 17 of the visual cortex via the LGN. There is another pathway. In order to raise the performance of the feedback loop employed to analyze fine detail presented to the fovea more effectively, a direct neural path has been created between the photoreceptors of the fovea and the PGN. The PGN, as defined here includes multiple elements of the thalamus, including the pulvinar. The PGN and the other elements of the Precision Optical System (also known in different communities as the Auxiliary Optical System, Auxiliary Optical Nucleus, the nucleus of the optic tract (NOT), or at least part of the Edinger-Westphal complex) compute the commands directing the ocular muscles. These computations are performed using additional signals from the vestibular system. This region of the brain also computes the commands for the iris separately. Pansky, et. al\(^{185}\) present the morphology of this region in some detail via a series of separate figures. They do not provide a sufficiently clear illustration of the correlation of areas of the retina to areas of the cortex. More recently, Nolte & Angevine have presented more details related to this area\(^{186}\). Grasse & Cynader prepared a comprehensive summary of the experimental data related to and the function of the AOS as it was known in 1991\(^{187}\).

As an alternate output of this servo loop, a set of vectors are created describing the fine detail in the presented image. These vectors are presumably transmitted to the primary visual cortex in order to fill the void, documented by Ganong, in the visual field transmitted to that location via the primary visual radiations.

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\(^{182}\)Humphrey, xxx (1972) xxx New Scientist, vol. 53


The literature prior to 1985 was at best speculative on how the information delivered to area 17 was passed on across the parietal-occipital sulcus to the higher cognitive centers. Similarly, little was reported concerning the passage of signals from the parietal lobe to the anterior lobe, although the fact that the signals in the pulvinar pathway, or secondary radiation, were demonstrated to be bidirectional.

The topology described above can be compared to a similar topology of parts of the human visual system provided by Miller. He focused primarily on the neuroanatomy of the midbrain portion of the system.

**15.2.5.2 Plan view of the visual topology of human and other primates, ca. ’98**

Figure 15.2.5-2 provides a plan view of the visual system compatible with the above profile view. The figure is complex and combines features found in several earlier, less comprehensive, figures by other authors. It is quite compatible with the simpler diagram of Slamovits & Glaser if it is recognized that their path to the “pretectal nuclear complex” supports the neurons from the entire

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foveola\textsuperscript{192}. It accentuates the symmetry of the system that is not stressed in Hoffman\textsuperscript{193} and expands the portions related to the cortex and the tectum to provide a more comprehensive view. This expansion also incorporates more detail with regard to the topology and topography of the cortex in the context of figures 114 and 116 of Bailey & von Bonin\textsuperscript{194}. The pretectal nuclear complex will be expanded into the perigeniculate nucleus and the thalamic reticular nucleus in the emerging plan view presented below. Graham presented a more morphological illustration containing the same elements based on Homan’s work in 1941\textsuperscript{195}. The figure by Uttal shows the multiple signal paths leading to the occipital cortex. Some of these do not go through the LGN and/or “visual cortex.” Szentagothai\textsuperscript{196} has presented an excellent simile by Shkolnik-Yarros (1961) to the above figure. It provides more detail in the cortical layers, including a direct connection from the pulvinar to a stellate cell in area 19 of the primate visual system.

\textsuperscript{195}Graham, C. et. al. (1965) Vision and Visual Perception. NY: John Wiley & Sons. pg 53
Figure 15.2.5-2 Recent topological plan view of the visual system. Heavy solid lines represent afferent signal paths. Dashed lines represent efferent signal paths. The thalamus and Tectum are shown as separate to emphasize their distinct roles. The medial geniculate nucleus, associated with the auditory system, is shown to stress the specialized functional role of this region of the Thalamus.

The figure is still diagrammatic. For purposes of discussion, the two Area 7's of Brodmann, divided by the medial plane, is shown folded down from its normal position directly above the thalamus and tectum to a position along side the thalamus in the plane of the paper. This causes the path-lengths from the PGN to be illustrated as longer than they actually are. The labels CE indicate the location of the sulcus centralis defining the anterior limit of the occipital lobe. The numbered areas of Brodmann, which are symmetrical with respect to the occipital lobe, are labeled on the right hemisphere.

This plan view also emphasizes the two separate and distinct bifurcations associated with the optic nerve of each eye. The first is found in the optic chiasm. The second is found between the chiasm and the termination of the
neurons in the LGN and the PGN.

The thalamus is shown as a saddlebag shaped structure containing three major nuclei and generally enclosing the tectum. The tectum is shown as a separate entity containing the left and right structures of the super colliculus, which are also paired about the centerline of the brain.

The figure is consistent with previous top level schematics of both the non-cortical and cortical portions of the visual system (See the next section). It shows a variety of signal paths that have been drawn to indicate their nature. The heavy solid lines represent afferent signal paths and the dashed lines represent efferent signal paths. Many connections have been omitted, including all association neurons between areas of the cortex, which are shown as lines of alternating long and short dashes in other figures. The figure is generally consistent with the emerging view of the human visual system but it lacks the necessary emphasis on the critically important functions of a central control point and a newer interpretation of the role of the occipital lobe of the brain. These shortcomings will be addressed in a similar emerging plan view of the visual system in Section 15.6.4.

15.2.5.2.1 Specific signal paths within the brain

It is necessary to use very precise language when discussing the signal pathways of the brain. Zeki addressed the subject in one sentence that is too brief. He said “there is no cortical region which is only recipient—all cortical areas have outputs as well as inputs.” More progress can be made if the terms afferent, efferent, projection and association paths are used. In this context, there are clearly afferent and efferent projection neurons terminating and originating in the cortex. There are also a large number of association neurons, of both short and long physical length, interconnecting the various perceptual engines and cognitive areas of the cortex. These association neurons appear to proliferate without end when interconnecting the various engines and cognitive areas. It is difficult to assign a afferent or efferent role to these neurons.

Slamovits has described the size of the optic chiasm in detail197.

The second bifurcations of the optic nerve are important in understanding the operation of the visual system. They initiate the separate pathways involved in threat detection (Awareness mode) and threat evaluation (Analytic mode) in the chordate visual system. As will be discussed below, the neural pathways proceeding to the LGN’s are primarily involved in awareness and threat detection. Because of the unique position of the LGN’s in the signal paths leading to Area 17, this path is also used to extract signals from the images presented to the retina for purposes of ocular steering and image merging. The neural pathways proceeding to the PGNs are primarily involved in threat evaluation and other abstract perceptual tasks.

Because of the separation of the initial visual data reduction process into two distinct fundamental processes, the detailed definition of afferent and efferent needs to be caveated. There are actually two locations in the brain which can both receive afferent signals and dispatch efferent signals. With respect to the visual system, these are the precision optical system at the juncture of the PGN/pulvinar couple and the superior colliculus, and within the cerebral cortex. Within the cerebral cortex, a large number of association paths are also encountered. Because of the star configuration of the data paths of the cortex, it is not generally possible to describe these paths as afferent or efferent. Their definition in these terms requires detailed knowledge of the engines they interconnect and the signal manipulation algorithms used by those engines.

The Precision Optical System is difficult to categorize biologically. It is to a large extent part of the autonomous nervous system. However, it accepts coarse steering commands from the cerebral cortex, a function normally

associated with the peripheral nervous system. It is proposed that the POS incorporates a central “control point” that coordinates all of the traffic between the pretectum, cerebellum and cerebral cortex. This functional unit is illustrated in many of the figures in this Chapter. Unfortunately, it is difficult to discern from the morphological literature whether the control point is part of the superior colliculus or the thalamus. This situation will be resolved in Section 15.6.

Afferent signal paths

The signals extracted from the servo loop of the Precision Optical System emanate from the combined PGN/pulvinar couple and the super colliculus of the midbrain area. These signals proceed along the pulvinar pathway to a feature extraction engine in areas 7. Robinson, et. al198. have described the functions and topography of area 5 and 7 in considerable detail although some language may be ambiguous. Within the immediate vicinity of area 7 are the feature extraction engines of the somatosensory system and possibly the auditory, limbic and other relevant feature extraction engines. It is well documented that the feature extraction engine in area 7 is associated with the response of the animal to changes in the object scene. It appears the feature extraction engines associated with these other systems are also in this larger area. As a result, the command assimilation function, relating to the control of the line of fixation of vision, including both the ocular and skeletal optokinetic responses, appears to begin in area 7 based on efferent signals from these individual sensory systems. The afferent signals from these engines in area 7 are transmitted to the various motor nuclei of the super colliculus. Note that these signals are not yet in usable form. They must be combined with other signals, such as those from the vestibular system in order to create a complete command signal suitable for the peripheral neuromotor system. A precise anatomical pathway between area 7 and the super colliculus, followed by these initial commands, was not located in the literature. If these signals share the anatomical pathway known as the pulvinar pathway, it is obvious how confusion as to the purpose of that pathway could result.

The fact that the commands assimilated within area 7 involve inputs from several sensory systems but are still not complete is highlighted in the paper by Robinson, et. al. They provide data for a matrix of inputs to and outputs resulting from the command assimilation engine supporting, but not generating, the complete optokinetic response. They stress their conclusion that the neurons of area 7 do not perform a “command function.” The quotation marks are theirs. It appears they would be comfortable with area 7 performing a command assimilation function but not the entire command generation function. It is suggested that the final command implementation function, within the super colliculus, can include other signal manipulation circuits that can modify or reject the afferent signals from area 7.

Robinson, et. al. also provide three other valuable perspectives. They stress the fact that area 7 does not exhibit a topographical representation of the retina. There is no reason to believe area 5 would exhibit such a topographical representation either. They also stress that they have not recorded any off-responses in parietal neurons. They included a discussion of the responses of humans and monkeys to operational deficits in area 7.

They also provided some useful information on the latency of the signals although they were not explicit as to whether the signals they measured were as received (afferent) or subsequent to signal manipulation by the various engines in the area of area 7. Although they did not describe the intensity or spectral content of their illumination, and appeared to have encountered some artifacts of the adaptation process, they did indicate a 4 ms. rise time for their optical shutter. Their results for the macaque indicated a median delay of 80-100 ms. based on a 20 ms. bin width. This data can be combined with the electrophysiological data of the retina and psychophysical data to determine the temporal aspects of the response to a stimulus by individual section of the sensor–cortical-motor response system.

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Efferent signal paths

Bidirectional pathways

Although a lesser problem, categorization of the pulvinar pathway is similarly difficult to categorize. It appears to support both afferent signal paths from the either the PGN/pulvinar or super colliculus to a feature extraction engine in Area 7 and efferent signal paths from an adjacent command assimilation engine in Area 7a to the super colliculus. There are probably many other undefined bidirectional pathways.

Because of the complexity of the neural pathways (signaling pathways) found within the brain (both mid and new sections of the cortex) and the density of signal processing within these areas, it appears that Zeki\textsuperscript{199} has given an unnecessarily narrow definition of these pathways. It still appears the location of various modular engines can be particularized topographically, as Zeki has been doing in the last five years (See Zeki’s 1999 and 2000 papers). He is also well aware of the role of the pulvinar pathway and the fact that signals reach the higher level perceptual areas and the cognitive centers without passing through V1 and V2.

15.2.5.2.2 Preliminary table of efferent paths to POS

The number of known signal paths is large and the number of undocumented signal paths is gigantic. Their existence, probable significance and the nature of the signals carried needs to be compiled in a comprehensive data base. Table 15.2.5-1 is offered as a sample of a flat file that could be incorporated into such a database. It describes a specific group of neural paths within the brain. This table provides a brief description of the neurons leading to the portion of the POS that generates the composite signals used to control the oculomotor nuclei that in turn control the line of fixation of the eyes.

Table 15.2.5-1

(A sample TABLE OF NEURAL SIGNAL ASSIMILATION)

<table>
<thead>
<tr>
<th>NEURAL PATHS BELIEVED TO SUPPORT THE GENERATION OF OCULOMOTOR COMMANDS by the SUPER COLLICULUS WITHIN THE POS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Source</td>
</tr>
<tr>
<td>-------</td>
</tr>
<tr>
<td>LGN’s</td>
</tr>
<tr>
<td>Area 7a</td>
</tr>
<tr>
<td>PGN</td>
</tr>
<tr>
<td>Vestibule</td>
</tr>
<tr>
<td>Tremor gen.</td>
</tr>
</tbody>
</table>

The table quickly illustrates the nature of the individual functions related to the POS. This table immediately leads to a need for a table describing the signals being assimilated in Area 7a. As a minimum, this area assimilates command instructions from area 7, from the cognitive centers including area 8 of the anterior cortex, and instructions from the occipital cortex (arriving from area 17 via area 18 and 19).

### 15.2.5.2.3 Comparisons with the literature

There are two major, and more recent, articles in close agreement with the above caricature. After exploring the definitions of vision and blindness (as also discussed in Section 18.1.2), Schneider described two visual systems in the Syrian golden hamster\textsuperscript{200}. His performance based results clearly support the description of the awareness, analytical and alarm modes of the above figure. The work is notable in its confirmation of an analytical mode in the hamster as well as the human (and therefore probably all—at least warm blooded—chordates). By itself, it is a clear indication of a foveola and peripheral retina in the hamster.

Trevarthen & Sperry have presented a figure describing two distinct “visual systems.”\textsuperscript{201} It is important to read the paper critically. The investigators eliminated the signaling path involving the foveola from their experiments. McGeer, et. al. did not recognize this fact when they reviewed, gave an interpretation of, and included an edited figure from Trevarthen & Sperry. As a result, they suggested the performance of the subjects was better the farther the tests moved toward the periphery of the retina. This was only true for the specific tests used. In fact, these subjects could read using their foveola. They were evaluated using the Wechsler Adult Intelligence Scale which is highly reading oriented\textsuperscript{202}. Rodman\textsuperscript{203} appears to have picked up the concept presented in Trevarthen & Sperry and perpetuated by McGeer, et. al. All of these interpretations show visual signals from the retina going to the superior colliculus before reaching the pulvinar. This work suggests the afferent signals go to the perigeniculate nucleus before passing to the pulvinar. The signals between the superior colliculus and the retina are efferent.

After blocking illumination to the foveola in a series of subjects who had commissurotomies, Trevarthen & Sperry still observed what they described as two distinct signaling paths related to the peripheral retinas. Their experimental results are in complete agreement with the operating modes proposed here. Their experimental procedure was more complex than required for the purpose of this section. They noted, for example, the close tie between the verbal production center, normally located in the left cerebral hemisphere, with the visual capability of the same hemisphere. They showed that though the corpus callosum was completely cut, the subject still reported verbally seeing moving and flickering objects in both hemispheres. They attributed this to a second visual pathway feeding back from the right hemisphere to the left hemisphere via the superior colliculus.

Their first pathway passes from the retina through the LGN’s to the Striate Cortex. The second is shown passing through the Superior Colliculus (based on morphology) to the Secondary or Association cortex.

Treffert & Christensen recent reported on a savant named Kim Peek who exhibits remarkable powers of memory and is known to be missing a corpus callosum entirely\textsuperscript{204}. Unlike many savants with great memory skills in a limited area, Kim exhibits great memory skills in a wide range of genre. Like many


\textsuperscript{201} Trevarthen, C. & Sperry, R. (1973) Perceptual unity of the ambient visual field in human commissurotomy patients. *Brain*, vol. 96, pp 547-570


\textsuperscript{203} Rodman, H. et. al. (1989) In Weiskrantz, L. Consciousness Lost and Found. NY: Oxford Univ Press. pg 129

\textsuperscript{204} Treffert, D. & Christensen, D. (2005) Inside the mind of a savant *Scientific American* vol 293, pp 108-113
other savants, Kim is unable to live alone successfully and is unable to button his clothes. Yet, he continues to improve his motor skills and has recently begun playing the piano. How well he plays was not specified.

At a greater level of differentiation, it is proposed that the neurons not going to the LGN’s go to an area of the thalamus labeled the PGN (directly). In this interpretation, the PGN and LGN are parts of the thalamus along with the Pulvinar. More importantly, there is a control point, defined further in Section 15.6, that controls the passing of signals (both alarm, analytical and volition) between the various engines of the visual and higher cognitive systems. Under this interpretation, figure 9 of Trevarthen & Sperry that they describe with the word “tentative,” can be simplified. This is best done after considering Section 15.6.1 (see Section 15.6.4.3.1).

The pathways associated with the “first” and “second” visual systems will be detailed below and in Section 15.2.5.4.

15.2.5.3 Expansion of the visual path architecture within the brain ca. ‘08

The previous figures have not provided meaningful information concerning how high resolution information is extracted from the scene by the visual modality. This information is associated with the small area on the retina associated with the point of fixation. This area is defined as the foveola, is defined by Maxwell’s spot (Section xxx), and is nominally 1.2 degrees in diameter. As noted above, the foveola and a major portion of the macular do not project to areas 17, 18 & 19 of the occipital lobe. **Figure 15.2.5-3** expands an earlier figure from Livingston & Hubel to show what is now known about the major functional paths of the visual modality. The signals from the individual retina divide into two distinct super-pathways, one proceeding to the LGN as discussed above and a second proceeding to the PGN. The super-pathway involving the LGN processes information related to the broad expanse of the external environment and is important to the safety and navigational ability of the subject. The super-pathway involving the PGN processes only information from a limited field of view determined by the state of attention of the subject. This is the area to which the analytical skills of the subject are directed. This small area is processed at a resolution at least 100 times higher than the peripheral regions of the retina.
Following processing within the two distinct super-pathways, the signals are passed back to the thalamic reticular nucleus (TRN) for combining and passing to the saliency map associated with the parietal lobe of the cerebral cortex. The sensory information stored by the parietal cortex are accessible by the cognitive circuits of the frontal lobe (stage 5).

The signals from the foveola are represented in the PGN of the figure by the word PRESS overlaid on a two-dimensional array. The means by which high resolution information is extracted from the signals delivered to the PGN, including how humans read, are developed in detail in Chapter 19.

The PGN is located between the LGN and the superior colliculus but is organized entirely differently. It is a small reticulated area of only a few million neurons. The neurons form a two-dimensional, nominally rectilinear, array on the surface of the PGN. The array may exhibit additional layers in depth.

The recent schematic of Dacey shown in Section 11.8.1 is compatible with this work and the extension of Hubel & Livingstone shown above. Dacey focuses more on histology than function.
15.2.5.4 The top level schematics of cortical vision

The organization of the cortex varies significantly between major phyla in order to accommodate the variation in topography of the animal. In *Arthropoda*, lower *Mollusca*, and lower *Chordata*, the eye is mounted firmly to the underlying body structure. In the more advanced members of *Mollusca*, there is one degree of freedom (although limited) between the eye and the head. There are two degrees of freedom between the eye and head of *Chordata*. The angular extent of these degrees of freedom vary considerably within the phylum. The Top level Schematic of the visual system in *Chordata* is presented again in Figure 15.2.5-4 [same as Figure 1.5.2-2]. A number of features of this figure need highlighting before continuing. First, it is seen that the eye in vertebrates is structurally and dynamically separated from both the brain and head (and/or body). Most of the other sensory input information is provided to the brain in a form that is uniquely described as to its source location on the skin and/or its characteristics relative to the position of the semi-circular canals of the inner ear. There are two important aspects of this difference in topography. First, there are two degrees of freedom between the eye and the head and six degrees of freedom between the head and the inertial reference of the outside world. The ocular globe is actually constrained by three sets of muscles. However, the oblique set are only used to correct for a lack of complete orthogonality between the other two. The eye shows no ability to roll about the line of fixation. Skavenski, et. al. have further delineated the skeletal platform into separate elements for the head and body in order to present their data. In general, the head shows three degrees of angular freedom relative to the body and the body itself can exhibit six degrees of freedom, although rolling about the line of sight is an unusual one.

There is a question to be resolved with regard to the above figure. What types of signal paths exist between the

---

various processing matrices of the retina and the enumerated locations in the brain of the animal? There appears to be a consensus in the literature that chromatic information, at least of the first order, is not presented to the PGN. On the other hand, McDonald & Hawryshyn\textsuperscript{206} provide data that chromatic information is present in the tectum of the rainbow trout. The eye of the fish is not as mobile as those of the primates.

The configuration of the Pretectum, Superior Colliculus and the interconnections between them is only shown conceptually in this figure. The functional roles assigned to these elements can be expanded as shown in Figure 15.2.5-5. This figure will be expanded further in the following sections. At this level, it shows the principle signaling paths found in the human visual system and their relationships. It also illustrates the major delays involved in the system related to the projection of signals over long distances by the Stage 3 circuits.

\begin{figure}
\centering
\includegraphics[width=\textwidth]{diagram.png}
\caption{Top level functional diagram of the cortical portion of the visual system. The emphasis is on those elements subsequent to the optic nerve.}
\end{figure}

In the upper left, the signals from the retina, divide into portions related to the foveola and those ex-foveola. The ex-foveola portion proceed through the upper awareness path to the LGN and onto the neo-cortex (area 17). The foveola portion proceeds to the PGN of the POS where they participate in a large variety of critical functions besides passing onto the neo-cortex via the analytical path (area 7).

Two important paths radiate from the LGN to the POS. These are the alarm mode paths and the stereo signal paths. The latter paths contain the coarse vergence control paths. The former paths contain the all-important alarm signals that can take control of the POS for a short period. It is this path from the ex-foveola (peripheral) retina that James wrote in the late nineteenth century when he said, “The peripheral retina is like a sentinel and when an object of regard falls upon it, it shouts ‘hark, who goes there’ and calls the fovea to the spot.”

Both the awareness and analytical path feed signals to the Parietal-Occipital-Temporal lobe junction area, POT. This area acts as the primary gatekeeper for both cognitive and command generation activity related to the neocortex. It controls the passing of information to the anterior lobe and the passing of the initial (highly condensed) instructions formed in that lobe back via the volition path to the old brain for command generation and execution.

The paths, related to the reflex mode, between the PGN/pulvinar couple and the cerebellum play a critical role in the higher chordates that goes well beyond simple skeletal motor responses to alarms. It appears to be the location of the extended memory required in higher chordates to recognize a wide variety of interps developed by the PGN/pulvinar couple. This figure will be discussed in greater detail in Sections 15.6.1 through 15.6.5.

Confirmation of this signaling geometry is provided by a discussion of blindsight in Bridgeman & Staggs. They report on a 27 year-old who suffered a severe traffic accident. He suffered a bilateral subdural hematomas over the occipital lobe (apparently excepting a small area of the left hemisphere within the calcerine sulcus). He was left with bilateral vision limited to a nine degree hemi-circle to the right, centered on the point of fixation. Yet, he was able to sense both moving and transient but stationary test targets introduced into his horizontal field of view over a range of ±45 degrees. He also experienced some macular sparing. The investigators did not define this condition. However, it usually constitutes a 1.2 degree circle of vision centered on the line of fixation and representing the operation of the foveola and analytical mode of visual operation. This appears to be a well documented case of nearly complete failure of the awareness channels (except for the hemi-circle) yet normal operation of the alarm mode and apparently the analytical mode. The test protocol called for the subject to use a manual device to point to the target rather than let the POS reposition the line of fixation to the target. As a result, a learning process was introduced beyond that normally associated with the alarm mode. The data must be interpreted in this light.

Additional discussion related to this figure appears in Stone. His foveal and ambient categories match well with the analytical and awareness modes of this work.

15.2.5.4.1 The major operating modes of the brain (related to vision)

The arrival of the man-made computer has led to the development of complex machines that can operate in a variety of modes simultaneously. The brain also operates in multiple simultaneous modes. Interpreting the available data (especially related to vision) allow many these modes to be defined. The modes can be defined from several perspectives. Some are apparent to the subject (conscious) and others are not (subconscious). Some are under cognitive control (volition) and some are not (reflexive). Some activity is limited to vegetative functions and some involves interaction with the environment. Some involve cognitive action in preparation for an action and some are based entirely on prior training. Development of the last dichotomy leads to an appreciation of the great importance of memory to the subject. Without constantly relying on memory, the subject becomes significantly less capable and eventually reaches a state of near total incapacity (illustrated by Alzheimer’s Disease).

This work has encountered a variety of neural system operating modes. Although far from comprehensive, the
following table helps to place them in perspective.
The nervous system and the sensory aspects of the eyes are always operative. However, they may be largely nonfunctional at times. These times are described by the label **STANDBY** mode. Dreaming is an example; the eyes are closed but the brain continues to manipulate data (particularly imagery) much as if the eyes were open and functioning. The neo-cortex continues to create commands directed at the motor (muscle) system. However, these are largely interrupted by the old brain.

Even when awake, the system can enter a semiconscious mode involving an apparently fixed stare (day dreaming). This will be described as the **STARE** mode. In both of the above modes, the fine motion of the eyes defined as tremor continues, as do a variety of other saccades.

When alert, the visual system exhibits three major operating modes related to sensing events in the environment. These are awareness, alarm and analysis. It also exhibits one mode generating pointing commands and actions that are not related to sensing. This mode is in response to cognitive action by the cortex and will be called the **VOLITION** mode. The interplay between this mode and the modes related to sensing is complex and highlights
the important role of the old brain. It is the old brain that decides whether to respond to volition generated commands or reflexive commands generated via the alarm mode.

While the **AWARENESS** mode is shared among all animals, the visual aspect of this mode is not. As the name implies, this mode provides the cognitive center of the animal with a description of the surrounding environment. This description is generally drawn from information from multiple sensors. It is global and inertially based. It is not related to the field of view of the eyes of the animal. In many animals lacking tremor as an oculomotor mechanism, other sensory channels are relied upon for most their sense of awareness. In at least the higher chordates, this mode exists at two operating levels. In the first level, the awareness is relative to the animal in a stationary inertial space. However, in many hunters, the system appears to be able to also operate at a pursuit level where the inertial space is centered on a constant velocity of the animal (at least temporarily). This second level is apparently limited in humans. While they can operate in a visual pursuit mode, this mode is quite limited.

The **ALARM** mode may be the fundamental mode of biological vision. It is shared by all known animals and generally leads to some degree of flight to escape potential threats. Failure to escape by flight can lead to a defensive posture. However, this posture does not appear to represent a separate mode with respect to vision. In man, the alarm mode appears to operate as several different levels in response to at least two distinct threat conditions. The simplest case involves the single threat level. There are two lower levels within this level. They relate to the naivete of the subject. In small children, the appearance of a threat for the first time may not generate any response. However, this experience can be considered training. On the second appearance of this same threat, the response may be significantly different. Through further training, the response can become quite sophisticated.

The second level within the **ALARM** mode becomes quite important within the sports and military regimes. It involves the ability to react appropriately to two or more simultaneous alarm conditions. The response to threats at this level is also a strong function of training. The degree of training frequently separates the successful player from the mundane players in sports.

The first order task of the alarm mode is to decide if the trajectory of an object in the scene will cause an imminent collision with the animal. If not, the threat is considerably reduced.

The **ANALYSIS** mode is most common among the higher chordates and most optimized, both physiologically and programmatically, among humans. The mode depends on the fovea for its operation. For humans, it is optimized for the even more restricted area of the foveola. The operation of this mode appears to differ significantly with respect to scene content.

For the scene, or non-symbolic image, the analysis mode appears to operate at one of two sub-levels. In the most general sub-level, the visual system performs a routine search of the field of view to analyze the characteristics of the scene of interest to the animal. This mode appears to rely upon previous images of the scene stored in memory to a remarkable degree. Through this reliance, the animal can restrict the time required to complete an evaluation of the scene based on a search. This type of analysis is encountered when a person enters a room for the first time. On subsequent entries, much less time is used to discover the features of the room. The second sub-level involves specific analyses, performed in response to a signal from the alarm mode, of a given scene element to decide whether it is a threat. These analyses go beyond the calculation of the trajectory of any object moving within the field of view. It seeks to determine the nature of the threat within a more precise context; does the scene element have big teeth?

For the symbolic image, there is a specific analysis mode limited almost entirely to humans. It involves the detailed analysis of fine detail related to small objects within the instantaneous image on the foveola. These objects can be small objects of art or technology but most often are symbols related to communications (letters and words). The first or routine sub-level relates to objects of previously unknown characteristics. This is the
typical analysis performed when a person picks up an unusually shaped rock or a sea shell on the beach. It is also
the analytical mode used when someone looks at a document written in a foreign language or script. The analysis
involves apparently random motions of the eyes within a few degree field of view. The amplitudes of many
individual motions are measured in microradians. These motions are frequently related to tremor and are not
random. They are programmed by the POS in accordance with memories associated with any similar object. To
construct a perception of the whole object, the eye performs a series of minisaccades, and if necessary small
saccades, to analyze the entire object. This mode involves a large degree of memorization of characteristics and
can be considered training.

There is a second sub-level associated with the analysis of symbols. It is strongly influences by training and
memory. It allows the human to evaluate a familiar member of a class of objects previously studied quickly.
Although not limited to text symbols, it is most recognizable in that context. This sub-level is called the “dumb
default” in studies of reading. It is based on training in the syntax and vocabulary of a given language. For a
language like English, written from left to right and where the first syllable of a word is usually important, the
fixation point of the eyes will jump to the right after reading a word. The point of fixation will land on or about
the third letter from the start of the word. This is known as the dumb default. The POS of the visual system will
proceed to analyze the group of letters imaged on the foveola and store its interpretation temporarily until the
remainder of the word is interpreted. Following sufficient time to analyze the first group of about five letters, the
point of fixation will move to the next syllable until it completes analysis of all of the syllables of the word. It
will then perform another dumb default to the start of the next word. At the end of a line of text, the point of
fixation will drop down to the left end of the next line. Again, it will land on about the third letter from the start
of the first word. The process will continue indefinitely. It is not clear at this time how the POS works. It may
only assemble the interpretations associated with one complete word and pass that information on to the higher
cognitive centers via the Pulvinar Pathway. Alternately, it may assemble the interpretations related to whole
phrases before performing a global interpretation and sending that interpretation on to the higher cognitive
centers.

The above process is known as reading, whether it is applied to alphanumeric text or any other symbology or fine
structured patterns.

In most of the above modes, individual tasks within a mode are separated by large, or at least small saccades.
The smaller minisaccades and the motions associated with tremor are usually performed within a given task.

15.2.5.1.1 Classification of the visual signal paths within the optic nerve of Man

Several authors have proposed tabulations of the signal paths represented in Figure 15.2.1-1. These tabulations
are all ca. 1980-85. Wiesel & Hubel have provided a widely discussed tabulation based on a target and surround
field mechanism using electrophysical recordings of psychophysical stimuli.209 Derrington & Lennie210 and
Derrington, Krauskopf and Lennie211 have proposed perfections to the definition of some of these types.
Unfortunately, most of these tabulations have been performed under psychophysical conditions using large area
test fields. Such large fields can obscure the details associated with these circuits. The illumination source used
by Derrington, et. al. also leaves much to be desired. They used a P4 phosphor cathode ray tube and interference
filters to select specific wavelengths. The P4 phosphor exhibits two spectral components and can not be
satisfactorily described in terms of color temperature. Such a phosphor appears white after adaptation by the

209Wiesel, T. & Hubel, D. (1966) spatial and chromatic interactions in the lateral geniculate body of the rhesus
monkey. J. Neurophysiol. vol. 29, pp. 1115-1156
nucleus of macaque. J. Physiol. vol. 357, pp. 219-240
macaque. J. Physiol. vol. 357, pg. 241-265
observing human eye, and probably all chordate eyes. However, it does not even approach white on an equal flux basis.

The two papers by the Derrington team provide many statements that appear to correlate well with the recent model proposed here. However, the approach is so different that it is sometime difficult to assign adequate precision to their statements. They rely upon curve fitting using arbitrary functions rather than a theoretical model. As an example, they say "We show that cells fall naturally into distinct and rather homogeneous groups: two chromatically opponent classes in the parvocellular layers and a separate magnocellular group." Considering the macaque as a higher chordate, this would agree with the model of this work precisely. However, there definition of the separate magnocellular group was less precise than for the parvocellular group. Did the magnocellular group include an opponent class? Similarly, their finding that chromatic difference pairs but no chromatic summation pairs are found in the parvocellular layers is in good agreement with this model.

A general conclusion from the work in this area is shown by Table 15.2.5-3

<table>
<thead>
<tr>
<th>From (matrix)</th>
<th>Ganglion type</th>
<th>Signal type</th>
<th>Signal content</th>
<th>Destination</th>
<th>Wiesel Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Luminance</td>
<td>Parasol</td>
<td>monophase</td>
<td>R-channel</td>
<td>PGN</td>
<td>?</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Foveola</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Non-foveola</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st Lateral</td>
<td>Midget</td>
<td>biphase</td>
<td>O-channel</td>
<td>LGN (Parvo)</td>
<td>II</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P-channel</td>
<td>LGN (Parvo)</td>
<td>II</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Q-channel</td>
<td>LGN (Parvo)</td>
<td>II</td>
</tr>
<tr>
<td>2nd Lateral</td>
<td>Midget</td>
<td>biphase</td>
<td>fine (\Delta R(s))-channel*</td>
<td>PGN</td>
<td>III-IV</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Foveola</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Non-foveola</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Coarse (\Delta R(s))-channel</td>
<td>LGN (Magno)</td>
<td>III-IV</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Velocity (\Delta R(s,t))-channel</td>
<td>LGN (Magno)</td>
<td>III-IV</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>? Other</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3rd Lateral**</td>
<td>Midget</td>
<td>biphase</td>
<td>polarization (1 or more colors)</td>
<td>? LGN (Parvo)</td>
<td>?</td>
</tr>
<tr>
<td>(or part of 1st)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* The differential refers to that between neighboring photoreceptors. \(\Delta R(s)\) is taken with regard to spatial position. \(\Delta R(s,t)\) is taken with regard to spatial position and a unit delay time.
** Not found in higher chordates.

It is probable that all of the neurons in the optic nerve associated with one of these paths are grouped together in order to make the rerouting, at the 1st optic chiasm leading to the LGN’s and at the 2nd (similar) chiasm leading to the PGN, easier. Ganong has mapped the location of the neurons leading to the PGN by sectioning the optic nerves. Derrington & Lennie have also noted the paucity of neurons related to the fovea in the magnocellular area of the...
LGN\textsuperscript{2}\textsuperscript{2}.

The Wiesel type refers to the characteristics of the neurons found in the LGN that receive these signals. Wiesel & Hubel were working at a relatively gross level involving large surrounds relative to the field of individual photoreceptors. In that sense, their designations exhibit an average or global character. They may only apply to more complex spatial encoding than discussed in this work. However, their results appear compatible with these path designations. Derrington & Lennie gave more precise definitions of these neuron types in 1984.

A major problem with the analyses in the above papers is their complete lack of data concerning the antidromic paths related to the orthodromic paths they studied or inferred from their experiments.

15.2.5.1.2 Further comparison of nomenclature of cell types OUTLINE ONLY

[This stuff from Derrington, et. al. Needs a lot of work I need to separate fact from psychophysics]  
[ rework significantly or omit to end of Section]

The four types are defined as:

[check Wiesel or Derrington paper for exact wording of these]

Type I: Center-surround organization and based on different spectral sensitivities between the center and the surround.

Type II: Cells sensitive to a difference between two spectral fields that are co-extensive (no spatially opponent fields). No luminance sensitivity.

Type III: Center-surround organization without obvious differences in spectral sensitivities.

Type IV: On-center units with no significant spectral sensitivity

Derrington, et. al. Speak in terms of the properties of the various cells of the LGN as opposed to the type of signals delivered to those cells. Their proposals are consistent with the view that within the LGN:

+ only the parvocellular portion receives (difference) signals related to the chrominance channels.

+ the magnocellular portion receives (difference) signals related to the luminance channel and probably serve to perceive moving objects.

+ no adaptation to signal levels occurs within the LGN.

They continued:

+ Most parvocellular layers had receptive field with XXX organization. They have chromatically opponent receptive fields and exhibit very low contrast sensitivity. (Pg. 238 & 239) No cells were found in the parvocellular layers that lacked chromatic opponent. They also noted the high ratio of parvocellular to magnocellular neurons representing the fovea in the LGN.

The temporal frequency response of cells in parvocellular layers extended up to 40 Hz. (Pg. 229)

+ All magnocellular layers had receptive fields with center-surround organization. Eighty-seven of 105 cells showed no apparent chromatic opponency and were labeled Type III. Eighteen were on-center units with a surround that was slightly more sensitive to long wavelengths and were labeled Type IV. (Pg. 231) The cells in these layers had temporal frequency responses as high as 60-100 Hz. No signal paths originated in the fovea. (Pg. 237)

+ The magnocellular cells responded to the flicker of the color television monitor but the parvocellular cells did not.

It is interesting to note that the fovea has no chromatic capability, because of the putative lack of cones in that area, and it should have no achromatic capability, because of the paucity of signals passed to the magnocellular region of the LGN from that region. In fact, the morphology of the photoreceptors is not indicative of their spectral sensitivity and the photoreceptors of the foveola are passed to the neocortex via the PGN. The signals from the foveola bypass both the LGN and the primary visual cortex on their way to the neocortex.

They concluded that the magnocellular cells reflected a sensitivity about three times higher than did the parvocellular cells. It appears a factor of two-to-one would reflect the differencing as opposed to the summing function.

Gouras has provided information recently on the nature of the signals processed by the LGN\textsuperscript{213}. However, the data is still highly conceptual.

### 15.2.5.2.2 Comparison with cat nomenclature

A system of describing types of neurons projecting from the retina to the brain has been studied intensely in cats. The Y/X/W classification system is based on a presumed relationship between functional types of retinal ganglion cells and their “conduction velocity.” Section 10.1.2.4.1 discusses the fundamental problems largely overlooked in developing this classification system.

The Y/X/W nomenclature appears intermittently throughout parts of the vision literature. Unfortunately, the nomenclature is based almost entirely on morphological paths and not on function. They are also based on the assumption that all optical neurons pass through the LGN. Thus, this nomenclature is based on a model that is not completely compatible with this work. Stone provides a comprehensive review of the work supporting this classification system\textsuperscript{214}.

In general, the X-cells in cat are described as emanating from medium-sized ganglion cells in the retina and proceeding to the parvocellular layers of the LGN. These neurons would correspond to the chrominance channels (P– and Q–channels) of this work.

The Y-cells are described as emanating from the large ganglion cells in the retina and proceeding to the magnocellular laters of the LGN\textsuperscript{215}. These would correspond roughly to neurons supporting the luminance channel (R–channel) of this work.

The W-cells are described as being poorly understood. They are not described in terms of their path but in terms of their receptive field, long “visual onset latency” and slow axonal conduction velocity. These relative terms are not terribly useful. However, the claim that they may project to the superior colliculus may be useful. These may be neurons used to aid in the steering of the line of fixation. They provide a signal describing a change occurring in a


\textsuperscript{215}Jain, N. Preuss, T. & Kaas, J. (1994) Subdivision of the visual system labeled with the Cat-301 antibody in tree shrews Vision Neurosci. vol. 11, pp 731-741
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particular area of the peripheral retina that should be examined. If true, these neural paths are part of the alarm mode of the block diagrams of this work. It remains likely that they only project to the SC via other nodes.

Stone has provided an alternate interpretation regarding the W-cells and possibly similar types. He discusses their projection to the pulvinar and supraclellulus areas.

So & Shapley have reviewed these cell types with respect to both the LGN and PGN. Henry has also reviewed these cell types, and compared them with the (S)imple and (C)omplex types introduced by Hubel. Both discussions remain largely conceptual. No graphics are used.

It appears the S and C cells of Hubel are the two primary types of cells involved in stage 3 of the visual process. The S cells appear to function as ganglion cells in the generation of action potentials. The C cells appear to function as what are called stellate cells in this work. They recover electrotonic signals from streams of encoded action potentials applied to their input.

15.2.5.5 Classification of the visual signal paths within the brain of Man

Work with the intent of moving beyond single path traffic analysis has progressed rapidly in recent years. By connecting the individual signal paths, based largely on anatomy, the more complex signaling networks of chordate vision are becoming more defined. These are supereceding the simple tabular representations like those of Rosenquist referenced above.

Recently, Kandel, et. al. have redrawn a block diagram of the human visual system starting at the lateral geniculate nucleus by Merigan & Mausell. The latter work was a graphical presentation of a selected part of a tabular presentation by Livingstone & Hubel. Van Essen, et. al. have prepared a similar block diagram showing the same familial relationship to Merigan & Mausell. Tovee has also presented a variant of Van Essen, et. al. However, he continued to show a figure with many missing or undefined paths. Brown has expanded the figure in Kandel, et. al. but did not specifically treat the foveola. The diagram was influenced by many considerations from the field of information and system theory but some of the assumptions concerning signaling are not adequately supported. The authors describe the article as a general hypothesis. It relies heavily on the conventional wisdom of the literature for support. The Pulvinar pathway is shown as undefined. Their graphic material is summarized in Miller & Newman. Their figure shows the FEF and both area 7a and 7b, as well as other nomenclature, explicitly. However, they do not detail their purpose. From a functional perspective, these areas are relatively primitive in the monkey compared to the human.

Figure 15.2.5-6 presents an adaptation and extension of these figures, primarily below the medial line, but adopting the premises of this work. The resultant figure remains quite complex but shows many critical relationships. It will

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be discussed in several of the following sections. A similar presentation covering other cortical functions appears in Heide, Kurzidim & Kompf226. The figure lacks quantification of the number of neurons, either absolute or relative, associated with each of these reported paths. Similarly, there has been no precise description of the characteristics of the signals passed over these paths. Another version of the rightmost portion of this figure has recently appeared227. However, this contribution is from a cortical physiologist. A more comprehensive version will be presented in Section 5.6.4 of this Chapter.

Distler, et. al. have recently provided a mapping of the cortex of Macaque mulatta that shares many features with the top half of the above figure228. Their work summarized a multi-year program describing many morphological paths obtained from dye tracers.

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Figure 15.2.5-6 Major feature extraction and servo signal paths of the visual system. See text for extensive discussion. Cortex and Thalamus portions adapted from Kandel, et. al. (2000) treatment they credited to Merigan & Maunsell (1993) that appeared in Livingstone & Hubel (1988) but originated as a table in Maunsell & Essen (1983) and in a more general diagram in Gross, Bender & Rocha-Miranda (1974).
What is known about the signal manipulation and data reduction carried out in the brain appears to be entirely consistent with this work. The material in Kandel, et. al. and in Merigan & Maunsell would be considerably more readable if there terminology regarding color information adopted the more specific Hering terminology associated with the New Chromaticity Diagram for Research presented in Chapter 17. Specifically, if they recognized the four specific and orthogonal colors associated with the Hering theory, red, blue (violet), yellow and aqua. It would be more helpful if they dropped the Hering notation and recognized the presence of the two actual orthogonal chrominance channels (that are not based on the Hering theory), \( P = \ln(M) - \ln(S) \), and \( Q = \ln(M) - \ln(L) \) with the mathematical caveat developed in Chapter 16.

15.2.5.5.1 General Overview TITLE & LOCATION

All visual signals arrive at the brain via the optic nerve shown at the bottom of the figure. Following an initial bifurcation at the 1st optical chiasm (not treated in this figure) they again bifurcate at the 2nd optical chiasm. The portion of the R-channel signal path associated with the foveola separates from the remaining signal paths and proceeds to the PGN located within the thalamus. The remaining signals proceed to the lateral geniculate nucleus, LGN, also located within the Thalamus. The LGN decodes the n-ary encoded information from the photoreceptors not located in the foveola of the retina. It then distributes the data via Meyer’s loops and the optical radiation to the primary visual cortex, V1. From there, the data is further processed and passed to a series of feature extraction engines located throughout the cerebral cortex. Their precise locations are only now being determined via PET and MRI analyses.

The signals from the foveola are passed directly, apparently without n-ary encoding or any encoding associated with stage 2, to the PGN which is a feature extraction engine located within a closed loop servo system that controls the motions of the eyes and collaborates in the control of the skeletal frame. These actions are performed to provide both the large angle pointing capability of the visual system but also to provide the tremor required to provide imaging based on a eye that is fundamentally a change detector and not an imager. To accomplish the above functions, signals from the vestibulocerebellum system are accessed by the PGN/pulvinar couple. The vestibulocerebellum system consists of a number of separate and distinct elements. Pansky, et. al. describes these elements and their location in detail229. The PGN/pulvinar couple, along with other nuclei of the Auxiliary Optical Nuclei (Precision Optical System) develop the individual servo signals required by the neuro-motor neurons of the Superior Colliculus in order to command the neurons and muscles of the oculomotor system. Commands are also transmitted to the eyelids, the iris and to other control centers controlling movement of the skeletal system230.

Taube & Bassett have recently delineated the signals associated with the auxiliary optical nuclei in the rat (where oculomotor motions are small relative to head motions)231. The neural signals generated look very much like those produced by the “resolver” of a servomechanism used in a ships sonar (where the ship is free to turn but the display is designed to maintain a true north reference at the top of the screen).

The PGN/pulvinar couple also derives precise feature information from the Foveola signals that are not available via other non-foveola photoreceptors because of the optical performance of the lens group. These signals are delivered to the cerebral cortex by a path whose definition is very limited in the morphological literature. However, such a path clearly exists since it is used to fill the hole recognized by Ganong and others as discussed in Section [15.2.5.2]. It is the path that accounts for the clinically observed phenomenon of “macular sparing.”

Historically, researchers have spoken in terms of a direct correlation between the scene and the organization of the visual portions of the brain. They have spoken of topographically equivalent maps between the scene and the surface of the brain, primarily the region of the occipital lobe known as the primary visual cortex. Although there is

a limited correlation (injection of a current at points below the surface of the cortex will evoke sensations of “stars” at different locations in the equivalent object scene), it is clear now that the primary visual cortex is not intended to “image” the scene acquired by the retina. The signals within the primary visual cortex are better described as first order vector representations of the image information. These vectors are considerably different than a mere expression of an amplitude and color of a given element in the object scene. As one progresses farther along the path to visual signal perception and cognition, these initial vectors are converted to more sophisticated vectors that have no relationship to the pixels of the original scene. The vectors are more similar to those used to describe Brezieri curves in a computer drawing program such as Illustrator by Adobe.

An important feature of the brain is that its signaling architecture follows that of the retina. Most of the signal manipulation is performed within the analog (electrotonic) signal mode. Only signals being passed long distances (greater than 1-2 mm) are converted back to binary mode (action potentials). This leads to the curious fact that the engineers and scientists like to describe their digital processors as “neural networks” on the outdated assumption that the signals manipulated within the processing centers of the brain were handled in binary mode. The brain performs most of its work in the mode of the old analog electronic computers of the 1940-60's.

All of the elements of the cerebral cortex and the thalamus shown in the figure are considered part of the perceptual subsystem as opposed to the cognitive subsystem of the brain. In this figure, the cognitive subsystem, which includes the saliency database, would be shown as a separate plane with elements receiving information, in vector form, over signal paths emanating from the various elements enumerated in the figure. Note that the perceptual subsystem contains many areas on the surface of the brain that are unrelated to vision. These would also provide signals, in vector form, to the cognitive subsystem, and in the same manner.

In interpreting this figure, the comment of Merigan & Maunsell in the caption to their figure 1 is crucial and should be obvious: “As in other summaries of visual pathways, many cortical areas and connections have been omitted.” They expanded on this statement in the text: “Some of these pathways can be seen in Figure 1, but many more exist. Figure 1, like almost all diagrams of the cortical pathways, shows a highly selected subset of areas and connections.” More explicitly, it should be said that many are yet to be discovered and defined. They suggest that the known number of connections between areas of the macaque cerebral cortex now number over 300 and the complete set provides no clear impression of two parallel pathways. Van Essen, et. al. quote a value of 305 and suggest it represents about one-third of all of the possible connections among roughly 32 defined areas of the cortex related to vision. Although the diagram of Merigan & Maunsell implies by its curvature that the specified areas were located along the dorsal and temporal sides of the human brain, V4 is not so located. It is actually located on the ventral surface.

The chromatic content of the signals carried by the signal channels within the various pathways has been a subject of consternation to many, particularly since a signal related to the M-channel (green) shows up ubiquitously. As noted in Livingstone & Hubel (1988), the parvocellular layers exhibit chromatic differences between two of the spectral input channels (although they couch their statements awkwardly in Hering terminology limited to “red,” “blue,” and “green” instead of the more definitive red, blue, yellow and aqua used herein. They also note that the magnocellular layers exhibit signals that sum the primary spectral inputs. They say that the magnocellular system is in effect color blind, although they recognize that it does not contain signals that can be represented as coming from a single broadband achromatic source such as is frequently attributed to rods. They note that the magnocellular system responds to differences in specific chromatic amplitudes but is blind under isoluminant conditions.

15.2.5.5.2 Species specific signals of the Optic Nerve

The optic nerve is shown delivering signals related to five different signaling channels to the LGN in the lower right of the figure. Two of these signal channels are shown as dashed lines. The O-channel involves the difference signals between the UV- and S-channels. It is rudimentary if present at all in humans but quite important in other species, even small chordates. The N-channel involves the difference between two separate orthogonally oriented
UV-channels that provide information concerning the polarization of the scene to the animal. This channel is not used in humans and probably not used in chordata. Not shown explicitly in the figure are the differential channels, Z-channels, associated with form, velocity and other geometric properties of the scene extracted within the retina of some animals. The Z-channels appear to play a minor or negligible role in humans. The 2nd lateral matrix of the human is quite limited in cross-sectional area in the human retina but can be significantly larger proportionately in other animals, such as the cats.

It is important to recognize the different role played by the 2nd lateral matrix of the retina and the resultant Z-channels delivered to the LGN in humans versus other animals. Experimental data related to the 2nd lateral matrix and collected from cats is probably not applicable to humans and other higher primates who did not evolve initially as predatory game hunters.

As discussed above, the gross nature of the signals passed to the LGN from the optic nerve have been determined by Ganong and others. Notably absent from this data stream are the signals associated with the foveola. Cut “d” in the figure represents the apparent location of where Ganong and associates cut the optic nerve. This location was after the 2nd chiasm. Because of this fact, Ganong did not correlate any signal paths associated with the foveola with his dissections. He left a blank cutout in his cross-sectional maps referred to object space.

Rodieck also recognized the presence of a 2nd chiasm which he discussed in terms of a minor input to the pretectum (PGN/pulvinar couple). He then noted with some consternation that after complete removal of areas 17 and 18, which essentially destroyed what he described as the X pathway, the cat suffered only a modest decrement in its visual discrimination ability (quoting Sprague). Clearly, the cat, being a higher primate with a well developed foveola and a PGN/pulvinar couple, processes its foveola signals in the PGN without relying on the LGN at all! In this earlier work, Rodieck describes an X and a Y pathway but employs different terminology based primarily on center-surround characterization rather than luminance and chrominance. The paper suggests some similarity between the X pathway and the summing pathway (M-pathway of others) after the 2nd chiasm.

15.2.5.5.3 The LGN and Primary visual cortex, V1

The LGN is shown as two groups of concentric circles. They have been separated from the actual six layer set of surfaces for convenience and are shown stylized relative to their normal morphological shape. The morphological details of the LGN are not important here. It consists of a six layer structure not unlike the area V1 to be discussed below. Livingstone and Hubel have provided a good review of this morphology. The important features to note are several.

Many introductory textbooks speak of the LGN in terms of relaying data on to the primary cortex. This description does not do justice to the LGN. As indicated briefly in the previous Chapter, the input portion of the LGN is part of the signal projection stage, stage 3, of the visual system. It is responsible for the decoding of the signals performed in Chordata to allow a smaller diameter optic nerve. This smaller optic nerve allows higher pointing agility in the ocular globes. The signal paths going into the LGN are shown as fine lines in order to represent the number of parallel neurons within each channel. The broad lines leaving the LGN signify the greatly increased number of neurons present after the decoding of the n-ary signals of the projection stage. These neurons are passed to the perception stage, stage 4, via the optic radiation that includes Meyer’s loops (not shown). Meyer’s loops appear to be a compensation for the length of the various ganglion axon lengths found within the retina as a function of field position. They provide a time delay as a method of compensation. This mechanism assures that all of the signals arriving at the primary visual cortex are in temporal alignment in spite of the relatively slow transport velocity of signals within the axoplasm of the neurons. The complex structure of the LGN is known to provide interdigitation of the signals from the two eyes. This complex morphological interdigitation of signals is almost surely accompanied by significant signal manipulation within the LGN.

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As discussed in Chapter 14, the signal projection function of stage 3 introduces significant asymmetries into the temporal signal characteristics of the differencing channels, including channels N-, O-, P-, Q- & Z-. These asymmetries are due to both the encoding algorithms used and probably to the characteristics of the circuit elements associated with the stellate cells. It is these elements that determine the time constants of the circuits used to recover the original signals applied to the input structures of the ganglion cell. This asymmetry becomes important below when separating the characteristics of the signal channels of the brain from the actual signals occupying those channels. This asymmetry is highly dependent on both the median and standard deviation of the wavelength and the amplitude of the signals in the chrominance channels as shown in Chapter 14. As a result, the “contrast” of the signals present at the output of the LGN are a function of both the wavelengths and amplitudes of the two original signals used to form the difference signal in the above channels. This makes the contrast a function of the state of adaptation of each of the spectrally selective photoreceptor types involved also. Statements about the contrast sensitivity of the signal paths from the LGN on must be precisely stated and recognize the above sensitivity to the input conditions.

In addition to its decoding function, the LGN interdigitates the signals from the fields of the two eyes and thereby prepares the data for further analyses. In this sense, it may be considered a feature extraction engine. However, it is probably best to consider it a formatting or fusion engine. In the following paragraphs, an “engine” will be used as a label to describe a region of the brain performing one or more specialized data manipulations leading to a less bulky amount of data but containing a higher degree of information. This is similar to the terminology currently used in computer science and the Internet. Each of these engines may occupy several square mm of surface area and involve millions of neurons.

Derrington, Krauskopf & Lennie have provided excellent data on the types of signals and features of those signals as found in the LGN of a macaque. The data generally supports the role of the parvocellular portion in processing differential signals associated with chromatic information in two distinct channels. The magnocellular portion appears to handle monopolar signals associated with luminance. This portion also appears to be associated with the processing of spatial information. It is clearly involved in processing orientation data relative to a grating and probably involved in both parallax and velocity merging functions. They found a good degree of linearity between the frequency of the action potentials and the input contrast up to about 0.3 contrast. However, the data was based on individual cells. This limited its statistical significance. They also found a significant paucity, or total lack, of signals originating in the central fovea in the magnocellular portion. This finding supports the position of this work that the cells of the foveola are connected directly to the PGN/pulvinar couple. They are not encoded for luminance and no luminance signal is transmitted to the LGN from the foveola. They said the parvocellular signals related to the fovea can resolve over 40 cycles/degree.

The primary visual cortex, Brodmann’s Area 17 and frequently labeled V1, is located at the extreme rear of the brain. It appears to perform two functions. It receives information from the LGN and distributes it to at least two engines (probably more) that begin the feature extraction tasks. It also appears that it performs some additional data reduction tasks. V1 is shown expanded to illustrate a variety of important features. First, the external surface of the brain is not a point of connection. All of the neural connections to V1 are made through the opposite surface near the layer labeled 6. This is typical of all elements of neural processing associated with the external surface of the brain. Each processing region can be conceived of as an electrical plug board as used in manual switching of radio and telephone connections. The sockets are all found on the face adjacent to layer 6 and the supporting circuits are behind the layer in layers 1 through 5. Local connections can be used using short length cables, association fibers,
with plugs on both ends. Longer distance connections are made with longer cables, projection fibers, going to remote electrical devices.

Livingstone & Hubel have proposed that the organization of area 17, V1, is considerably more complex than suggested by this figure. They show the structure as three sets of intersecting sets of planes, the layers shown, an orthogonal set of planes representing the left and right visual fields in a repetitive arrangement, and a second orthogonal set related to the orientation of individual test objects/patterns.

All of the interconnections shown in this figure are external to the individual engines and are carrying binary signals. In the case of every block (engine) shown, the signals are received in binary mode, decoded to analog mode, processed and then re-encoded in binary mode for transmission (unless they are to be sent over distances small with respect to 1-2 mm). If a particular engine is large, signals may be re-encoded for transmission across the area of that engine. In that case, the signals follow the path shown by the association fibers on the right of V1. Notice that such signals may be separate from the main fiber at various layers within V1. When traveling between engines, they are considered projection fibers (just as are those between the retina and the LGN). The individual neural paths traveling within a fiber may similarly separate from the main bundle and individual axon elements may separate from the parent axon in order to make synapses with the target neurons in various layers of the target engine.

The area of the cerebral cortex occupied by the various engines (block) shown in the figure involve several square millimeters to the size of V1 (square centimeters). Even an area of one square millimeter typically includes 10 million neurons. Such a large number of neurons represents an unimaginable capability for signal manipulation and reduction associated with each engine, even if performed in the analog mode.

V1 has been studied quite extensively and the references already given in this Chapter should be adequate for most readers. One of the important points is that the projection and association fibers are typically received at layer 4C, in 4Cα from the magnocellular laters, and in 4Cβ from the parvocellular layers. According to Hubel237, the signals leaving area V1 typically leave from layers 3 and 4B if going to other areas of the visual cortex and from layers 5 and 6 if going to other “deep structures” of the brain. The label deep structures probably correlates with the cognitive centers discussed in Section 15.2.1. These deep structures collect the information from the various feature extraction engines in order to create the saliency database required for purposes of cognition. In this respect, it can probably be assumed that all signals leaving for the deep structures depart from layers 5 and 6 of all of the elements in the figure and proceed out of plane.

The subject of blobs and interblobs will not be addressed here238. There are many structures within the human brain that are not understood functionally. These features appear to be among them.

15.2.5.5.4 Alternate connections between the retina and visual cortex

It has become clear from several investigations that the signals associated with the foveola do not travel to the primary visual cortex via the LGN. It appears these signals do not pass through the primary visual cortex at all but proceed via an alternate route through a region adjacent to the superior colliculus to the inferotemporal lobes (inferior temporal gyrus). This area also be considered an extension of the LGN and will be described as the pregeniculate nucleus (PGN) in this work. With this nomenclature, this path can be described as passing from the retina to the PGN to the pulvinar region of the thalamus and finally to the inferotemporal cortex239. Zeki documented this fact in his early work with the monkey240. Details related to the actual situation have been reported since the 1930’s. Figure 15.2.5-7 shows explicitly that the signals from what he describes as the macular proceed directly to

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the association areas anterior to Area 19. It is often described as the pulvinar pathway. It is considered a part of the tectal system, or secondary visual system. Zeki & Moutoussis describe it as the retino-tecto-cortical branch\textsuperscript{241}. Nolte labels it the association pathway. The purpose of this pathway has not been understood\textsuperscript{242}. In this work, it is clearly associated with the precision scanning of the image presented to the foveola in order to achieve a more precise level of perception. In the context of this work, the pathway would also include the PGN/pulvinar couple as a way point between the retina and the super colliculus. This pathway is a second output signal pathway associated with the servo loop formed by the precision optical system. The pulvinar pathway is shown in [\textbf{Figure 15.2.2-2 & Figure 15.2.5-2}]. Zeki & Moutoussis describe this pathway as bypassing V1 and reaching V5 at latencies of about 35 ms. They were not explicit as to whether the path bypassed V4 also. They did not describe how much of the above latency was related to transit time within the retina, along the optic nerve, or within the super colliculus. Earlier reports suggest the pulvinar pathway connects the PGN/pulvinar couple (or pretectum) to both the posterior of the temporal lobe and to the middle and rostral portion of the temporal lobe.

\begin{figure}[h]
\centering
\includegraphics[width=0.5\textwidth]{figure.png}
\caption{A caricature of the projection of the foveola and macula into a portion of the prestriate cortex of monkey (presumed to be the equivalent of area 7 in human). It is the peripheral retina that maps into the striate cortex of area 17, on the right in the figure. From Zeki, 1969.}
\end{figure}


While Hubel has argued (pg 134) that the striate cortex assigns a large part of its area to mapping the fovea, this position needs further explanation based on the imagery of monkey obtained by Tootell. Figure 15.2.5-8 shows one half of the total striate cortex, e. g., the portion associated with one of the cerebral hemispheres. The figure shows the nominal point of fixation as a circled star. The periphery from upper left around to the lower right describes the vertical meridian in object space. The left side of the triangular surface represents the edge of the striate cortex. In object space, this roughly straight edge represents a semicircle in object space approximately seven degrees from the fixation point.

In the above figure, the point of fixation is not on the edge of the operculum (flap) representing the contralateral field of view. Therefore, it provides a different interpretation than that of Zeki. There is no continuum of the foveola, or fovea, extending into the left quadrant of Zeki. Nor is there any common point of fixation shared by the two halves of the striate cortex. A broader discussion of the striate cortex will be found in Section 15.2.5.7.

Figure 15.2.5-8 An autoradiogram of one half of the striate cortex of *Macaque* monkey. The point of fixation is shown by the circled star. The vertical meridian projects from the upper left, around the point of fixation, to the lower left. The relatively straight line from upper left to lower left represents a semicircle in object space at approximately 7° from the point of fixation on one side of the vertical meridian. Compare to similar arrangement in the caricature of Figure 15.2.5-6. From Tootell, et. al., 1988.
As described in Section 15.2, there is a significant problem in the labeling of the cortical elements of the visual system. This is particularly true of the elements in the region of the thalamus related to the visual system. There is a secondary visual system, an auxiliary optical system, an auxiliary optical nucleus, auxiliary optical nuclei, and many other variants used in the literature for essentially the same inadequately understood functional elements. These elements are absolutely crucial in humans. As a group, they will be called the Precision Optical System in this work.

If the signals from the individual photoreceptors of the foveola are passed directly to the PGN/pulvinar couple without matrixing to form a luminance signal, it is interesting to consider whether this summation function is performed within the couple before the information is passed over the pulvinar pathway to the feature extraction engines of the cortex. If it is, the information would appear in the same form as that arriving at the primary visual cortex. Alternately, it may be processed to look like the information leaving the primary visual cortex. From an architectural perspective, this causes no difficulty. The summation can be done just as it is done by bipolar neurons of the retina. The processing within the couple or super colliculus may emulate the processing of the luminance matrix as well as that in the LGN and the primary visual cortex. Insufficient information is available to speculate in this area.

The putative signal path from the supercolliculus to the feature extraction engines of area 18 and beyond provide an obvious explanation for a well documented situation. It has been found that both cats and monkeys suffer only marginal loss in visual capability when the entire primary visual cortex is destroyed or removed244. Although the experimenters used less than precise language to describe this situation, the results were clearly surprising to them. Based on this work, the foveal portion of the visual system could be expected to remain viable because of the pulvinar (or secondary summation—see below) pathway. The capability of the visual system related to the peripheral retina would be expected to be seriously impaired under these circumstances.

15.2.5.5.5 Selected pathways of the occipital cortex

Authors, particularly of textbooks, have frequently attempted to describe the architecture of the interconnections between regions of the brain simplistically. They have assigned the elements labeled the middle temporal area (MT), the middle superior temporal area (MST) and 7a to a single signal path and labeled it the dorsal, or parietal, pathway. They have assigned the elements labeled AIT, CIT, PIT and V4 to a second pathway labeled the ventral, or temporal, pathway. These two pathways have then been discussed in terms of their parallelism without serious discussion in what sense they are parallel. They have also attempted to correlate these pathways with the so-called M- and P-pathways.

Note the terminology dilemma posed by the use of the letters P and M. The non-foveal portion of the R-channel extends from the Parasol ganglion cells to the Magnocellular portion of the LGN. The N-, O-, P- & Q-channels extend from the Midget ganglion cells to the Parvocellular portion of the LGN. There is also potential confusion between the so-called parvocellular pathway and the pulvinar pathway if only the letter P is used as an abbreviation. It would be best to rename these major pathways. It is suggested that the so-called M-pathway be renamed the Summation signal pathway and the P-pathway be renamed the Differential signal pathway. All of the differential signal channels of vision are included within this D-pathway regardless of species. All of the summation signal channels are included within the S-pathway up to the 2nd optical chiasm where the foveal luminance signal separates in the higher chordates. It is suggested that this separate pathway associated with the foveal luminance information be labeled the S' pathway or auxiliary summation pathway. Other authors have discussed the major signal pathways leading to the LGN in terms of X and Y pathways and labeled the source ganglion cells A and B cells. Pages 3418-

244Merigan XXX (1986 and 1993)
3419 of the Livingstone & Hubel paper discuss the similarities and differences between these sets of labels from a conceptual perspective. Lack of precise definition of the parameters in this area is a problem.

There has been little success in cross correlating these pathways. Merigan & Maunsell conclude: “Collectively, the available data . . . suggest that the original notion of parallel visual subsystems that extend from the retina to higher visual cortex must be extensively modified. The mapping between the subcortical and cortical pathways is not simply one to one.” From a signaling architecture perspective, it seems highly unlikely that either the perceptual or cognitive subsystems would be organized in such a linear manner. The linear or parallel manner is native to the projection of signals and is entirely appropriate to the projection stage of vision. However, it is generally not found in systems processing information, such as stage 2, 4 or 5 of vision. In these areas, the interconnection of processing locations is inevitably based on one of three typical architectures, the hub and spoke, the star or the ring. Each of these architectures offer different secondary features but they all outperform any parallel architecture. Review of the tectonic nature of the cortex as well as conventional signaling system design rules would suggest the brain operates based on a star network configuration. The architectural assumption that the brain is organized as a star network is supported by Van Essen who found at least 84 identified or suspected paths between 19 visual areas. Although not near the total number of possible paths in a star, it is far more than required by either a ring or hub organization. The assumption of a star network as the fundamental organization of the brain does not prevent individual authors discussing and developing specific paths through various elements of the star. It only insures that the overall context of the discussions is preserved.

Whereas Merigan & Maunsell provided a simple topological block diagram based on two parallel paths, Handel, et. al. converted their drawing into a more stylized perspective drawing implying a topography as well as a topology to the cortical elements of the visual system while retaining the parallel intimation. The above figure was intentionally drawn to not do that. Whereas Handel, et. al. showed paths crossing between the two parallel paths and some paths skipping around elements in one path, the above figure presents a more general view. It also recognizes, as did the caption in the paper by Merigan & Maunsell, that man has not yet discovered all, or probably many, of the elements in the perceptual subsystem or the interconnections between these elements. Under these conditions, it is safest for the researcher to assume a more general architecture. Generally, the star architecture is the most flexible. It allows direct access between any two elements and the addition of new elements. Unfortunately, it is not the most economical in terms of total interconnection path length. Also it suffers exponentially if new elements are added that must connect with all other nodes of the network. In the visual system, two points should be noted. Not all nodes must connect with all others, and the system can employ the third dimension for additional connections, particularly to the cognitive subsystem. Lacking further information, the star form is taken as the underlying architecture of the perceptual subsystem of vision in the above figure.

Writing at about the same time, Gegenfurtner & Hawken provide a good summary and list of references to the literature on the discrimination between color and motion signal processing pathways. However, their work is based strictly on psychophysics, with a few point-specific physiological measurements. They never mention the color temperature of their measurements. As customary in their community, they dismiss the role of the P–channel of color vision because of their use of inadequate light sources. They also overlook the limited low temporal frequency response of the signaling channels due to the adaptation mechanism. No discussion of the separation of the foveal signal processing from that of the peripheral signal processing is introduced. They associate the luminance (R–channel) signal processing with the MT. Simultaneously, they exclude processing of the Q–channel signals within the MT. While these conclusion are consistent with the above authors and this work, they are at the same time superficial based on this work.

There is an additional complication in the attempt to correlate the two types of pathways in the optic nerve with two pathways in the cortex. The original tabulation in Livingstone & Hubel defined three major pathways leaving the LGN. Artistic and authors license was used by Merigan & Maunsell to reduce this to two pathways by showing the thin stripe and interstripe paths leaving the same layer of the LGN and both entering the same element of V2. Livingstone & Hubel characterized these three paths as supporting signals with significantly different properties. In general, they conclude that the thick stripe path exhibits properties associated with the orientation of object(s) within the original scene and with stereopsis, the thin stripe path exhibits properties associated with the chrominance information about the object(s), and the interstripe (or pale stripe) path exhibits properties associated with the motion characteristics of the object(s). They specifically mention that the interstripe path did not show significant sensitivity to a flashing stationary stimuli.

The conclusions of Livingstone and Hubel were based primarily on center-surround and equiluminescent grating experiments of either their own or those found in the literature. Some of the center and grating illuminations were only 1/2° in diameter which suggests the surround included part of the foveola and the remainder of the surround was ex-foveola. They also noted the less than ideal chromatic content of the P22 monitor they used in their experiments. These situations can complicate the data reduction considerably, especially since it is not known how much of the complete data set for foveola pixels bypasses the LGN altogether by proceeding to the PGN. They point out that there are significant conflicts in the data base they located in the literature, all from the 1979-83 time period.

Their terminology frequently suggests that it is specific neurons (or groups of neurons) that are fast or slow depending on the function of the neuron(s). They do not make an attempt to distinguish between the signal capacity of the neurons and the characteristics of the signals being carried by these neurons. They also do not recognize the likely hood that the speed of response of the signal in a given channel might be a function of intensity or of wavelength as predicted by this work. They do note the considerable variability of the response of different individuals without any discussion of the state of adaptation of the individuals being compared. It is suggested that the above paper, and their earlier papers, can produce additional important technical information through data mining based on the theoretical model presented by this work. A similar situation exists with Table 29-1 of Kandel, Schwartz & Jessell 248 with the caveat concerning the labeling of the cells. M cells in that table are Parasol ganglion cells, P cells are Midget ganglion cells.

Their determination that the spatial resolution of the magnocellular pathway is significantly poorer than that of the parvocellular pathway would not be surprising if the direct signals from the foveola to the brain went to the PGN and did not appear in the LGN as proposed here. Only more detailed experiments can confirm whether these signals were delivered by the PGN to area 17 and were part of the subsequent signal manipulations of the engines shown in the figure.

15.2.5.5.6 Expansion of the visual path architecture within the brain circa 2008

The previous figures have not provided meaningful information concerning how high resolution information is extracted from the scene by the visual modality. This information is associated with the small area on the retina associated with the point of fixation. This area is defined as the foveola, is defined by Maxwell’s spot (Section xxx), and is nominally 1.2 degrees in diameter. As noted above, the foveola and a major portion of the macular do not project to areas 17, 18 & 19 of the occipital lobe. Figure 15.2.5-9 expands an earlier figure from Livingston & Hubel to show what is now known about the major functional paths of the visual modality. The signals from the individual retina divide into two distinct super-pathways, one proceeding to the LGN as discussed above and a second proceeding to the PGN. The super-pathway involving the LGN processes information related to the broad

expanse of the external environment and is important to the safety and navigational ability of the subject. The super-pathway involving the PGN processes only information from a limited field of view determined by the state of attention of the subject. This is the area to which the analytical skills of the subject are directed. This small area is processed at a resolution at least 100 times higher than the peripheral regions of the retina.

Following processing within the two distinct super-pathways, the signals are passed back to the thalamic reticular nucleus (TRN) for combining and passing to the saliency map associated with the parietal lobe of the cerebral cortex. The sensory information stored by the parietal cortex are accessible by the cognitive circuits of the frontal lobe (stage 5).

The signals from the foveola are represented in the PGN of the figure by the word PRESS overlaid on a two-dimensional array. The means by which high resolution information is extracted from the signals delivered to the PGN, including how humans read, are developed in detail in Chapter 19.

Figure 15.2.5-9 An expanded architecture of the visual modality within the CNS. Signals from the foveola are passed along the upper super-pathway for high resolution information extraction by the PGN/pulvinar combination. Expanded from Livingston & Hubel, 1988.
The PGN is located between the LGN and the superior colliculus but is organized entirely differently. It is a small reticulated area of only a few million neurons. The neurons form a two-dimensional, nominally rectilinear, array on the surface of the PGN. The array may exhibit additional layers in depth.

15.2.5.6 Task performed within the LGN & PGN

[xxx expand to treat both PGN and LGN and include operating mode labels, alarm etc. ]

The role of the LGN is critical to the performance of many tasks within the visual system. Its most obvious role is the merging of the signal information received from the two eyes into a single set of composite signals that can be processed further. As part of the task of merging the above signals, it extracts a set of signals used in the POS to support the generation of both version and vergence. It also appears to extract a set of values related to each target in the visual field that support coarse stereopsis.

15.2.5.6.1 Preparation for color perception

Recent work by Romney et al. have shown that the differential signals generated in the O, P & Q channels of the retina are delivered to the LGN in undistorted form\textsuperscript{249}. These discrimination functions are shown by the heavy lines (both solid and dashed combined) in Figure 15.2.5-10.

Figure 15.2.5-10 Raw chrominance signals delivered to the LGN before restriction appropriate to the spectral discrimination process. The raw inputs are shown by the heavy lines (both dashed and solid portions). To avoid the generation of spurious signals, the signals need to be restricted to the regions shown within the unshaded areas (the solid heavy lines only). Straight lines have been added to suggest how linear the discrimination functions are within the selected regions. The limitation placed on the input signals by lens absorption in humans and other large mammals is shown by the hatched area.
This figure shows the discrimination functions found in all members of Chordata (e.g., birds, fish, mammals, etc.). It is appropriate for large mammals, such as humans, when the absorption of the lens in the near UV is introduced. This absorption is shown by the hatched area of the figure.

Close examination of the signals received from the optic nerve are not yet in a form that can be used for color discrimination without additional signal manipulation. By analogy with a frequency discriminator in a man-made radio, it is necessary to limit the frequency (wavelength) range of the signals to the region of the discrimination function between the two peaks (the unshaded area) to avoid the generation of spurious signals (commonly known as splatter). While how this limiting is accomplished is not known at present, it is suggested that this is not an overly difficult task circuit-wise. This is particularly true because of the availability of brightness information in the adjacent magnocellular layers of the LGN. Generating a pedestal from the brightness information for each of the chrominance channels would accentuate the linear region (solid lines) of each signal at the expense of the spurious signal generating (dashed lines) portion.

Following the crude spectral windowing suggested above, the resultant signals are in the ideal form for supporting the Perceptual Chromaticity Diagram developed in Section 17.3. This Perceptual Chromaticity Diagram forms the foundation of the Hering or Opponent-Color Theory of human vision. It also provides the foundation for explaining the creation of the Munsell Color Space.

15.2.5.6 Important topological features of the LGN & PGN

[xxx refer to more extensive discussion in the chapters of “The Electrolytic Theory of the Neuron” and probably move this material to that work ]

The topology of the LGN and PGN in cat has been studied extensively, including its morphological relationship with the adjacent PGN. Unfortunately, it requires an experienced morphologist to interpret the many disparate views of the cat LGN in the literature.

Guillery has provided very detailed but early information on the cytology of the LGN in cat250. Many of his electron microscope images show multiple regions of significant electrical charge. He provides some data on the routing of the neurons between various laminae but does not coordinate his findings with the M and P pathways.

Steriade, et. al251., Lindstrom & Wrobel252 and Sanchez-Vives et al253. have provided excellent material on the topology and physiology of the cat LGN. Figure 3C in Sanches-Vives, et. al. Can be correlated with other physiological plots thereby allowing the correlation of the A, A1 & C layers with the M & P channels of the retina and optic nerve.

Many of the waveforms shown in these papers are electrotonic.

Lindstrom & Wrobel confirm the binocular merging performed within the dLGN, and particularly within the interlaminar layers (p.65). They also address the antidromic neurons originating in the cerebral cortex and

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251Steriade, M. Pare, D. et. al. (1989) Phasic activation of lateral geniculate and perigeniculate thalamic neurons during sleep J Neurosci vol 9(7), pp 2215-2229
terminating in the LGN. They also explore the relationship between LGN and PGN neurons.

15.2.5.7 Important topological features of the striate (visual) cortex

[xxx See also Section 15.6.5.3.5 for analysis of Tootell et al. work ]

Van Essen has provided the clearest and most definitive description of areas V1 (area 17) and V2 of the primate visual cortex\textsuperscript{254}. He lists five characteristics of V1;

1. It has a distinctive architecture based on a variety of staining techniques.

2. It receives highly specific inputs from the lateral geniculate nucleus.

3. It has an orderly and complete representation of the contralateral visual hemifield.

4. Its constituent neurons have well-defined receptive field properties that are characteristic of each cortical layer.

5. Lesions of it produce virtually complete scotomas, or perceptual blindness over the corresponding portion of the visual field.

He omits a sixth characteristic;

6. It incorporates many elongated neurons that lie parallel to the surface of the body and give it its characteristic striations.

He notes the awkwardness of using the term V2 since it contains at least five topographically distinct visual areas. Area 18 is only one of these.

In 1988, Tootell, et. al. published a very large amount of new and detailed information on the striate cortex of Macaque monkey based on an autoradiographic technique\textsuperscript{255}. Their work has continued to this day. However, the subsequent work will not be addressed here. The technique involves measuring the uptake of glucose with respect to spatial position using \textsuperscript{14}C-2-deoxy-d-glucose (DG), see Section 7.7.5.1. It is sufficiently precise to allow determination of the uptake for individual layers of the cortex, to determine local magnification factors for the cortex relative to object space, and to make some measurements relative to the finest spatial resolution achievable by the cortex.

The tootell, et. al. material is divided into five major sections (with the applicable page numbers);

I Ocular dominance, binocular interactions and baseline conditions 1500-1530
III Retinotopic organization. 1531-1568
III Color 1569-1593
IV Contrast and magno-parvo streams 1594-1609
V Spatial frequency 1610-1624

15.2.5.7.1 Mapping (conformal transformation) from object to striate space in Macaque

Figures 2, 3 & 4 (pgs 1535-37) of Tootell, et. al. provide significant information on the transformation from object space (not retinal space) to striate cortex space in Macaque, at least for the central seven degree circle of the field of view centered on the point of fixation. The figures are immediately suggestive of a conformal transformation of the parabolic form. Figure 15.2.5-11 reproduces their figure 2 in modified form along with such a parabolic


transformation that has been rotated and mirrored to form two lobes. This figure is also presented in more diagrammatic form in Figure 18.8.2-7. The lobe on the left has been mirrored to create a profile view from the rear of a flattened striate cortex. How the operculi were flattened has an impact on the overall figure. The hatched line along the upper and lower periphery of each real lobe represents the vertical meridian in object space. The hatched line with the heavy dotted extension represents the horizontal meridian. The vertically aligned hatching represent circles of constant radius in the field of view. A shaded area has been added to represent the void between the two quasi-hemispheres of the occipital lobe. The area within the dashed lines represent the extensions of the operculums into their medial surfaces. For the monkey, the visuotopic projection enters the sulcus at about 11° from the point of fixation.

Cowan256, based on the 1977 work of Schwartz257, has described the transform applicable to Tootell’s (and earlier worker’s) imagery as a complex logarithmic transform. This type of transform was considered initially in preparing this work but the complex parabolic transform appears to fit the situation more precisely. The analysis by Schwartz is largely conceptual and somewhat superficial. It suggests infinite magnification at the point of fixation and the horizontal lines in his Table 1 do not fit his cortical hemisphere in Figure 1C. The area of Figure 1C in the region of

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the dashed lines is not correctly portrayed. Schwartz revised his baseline in 1980\textsuperscript{258} and called for a different complex logarithmic transform incorporating a sum in the w-plane expression for \( z \) to alleviate some of the above problems. Figure 1 in the new paper also exhibits problems. Schwartz was forced to limit his representation to the central 20-30\(^{\circ}\) of the visual field. The complex parabolic transform proposed here does not suffer from these limitations. Stewart apparently interprets Cowan in his 2011 book for the popular press\textsuperscript{259}. However, Stewart’s figure 44 is inappropriate. That figure purports to show the human retina-topic projection with a common foveola area in the cerebral fissure. In fact, his figure 43 is the correct representation both mathematically and topologically. It shows insignificant partial representations of the foveola appearing behind each ear. The high magnification representation of the complete human foveola occurs within the diencephalon, not the cerebral cortex. As noted in the above caption, the mathematical form is the parabolic conformal transform. The topology does not involve any oval representation. The transform representation on each surface of the occipital lobe disappears into, and ends, in the cerebral fissure.


Anderson has provided a first hand report on the conformal transformation employed in human vision\textsuperscript{260}. He was surprised to find that he perceived circular lines in the peripheral field of the retina as straight lines. This follows directly from the conformal transformation described diagrammatically in Figure 18.8.2-7 from Tootel and Figure 15.2.5-11 above for the monkey.

As part of his treatment for a detached retina, a small bubble of air was introduced into his eye between the vitreous humor and the retina. He found this nominally oblate spheroid would move around over the surface of his retina as he moved his head/eyes. With a little practice, he could move the presumed circular edge of the bubble across the blind spot area of his retina. The result was not what he expected based on the common wisdom.

Figure 15.2.5-12 shows the sketch from Anderson. The common wisdom is that a circular disk projected so as to move over the nominally circular blind spot (dashed circle) at about six degrees from the point of fixation should be obscured much as the sun is during an eclipse. However, this is not what he actually perceived.

The circular disk projected onto the retina as well as the blind spot are projected onto the cerebral cortex as quasi-rectangular features. As such the projected disk (which should be shown as a quasi-rectangular object) disappears as in (b) as if it encountered a linear edge of an obscuring rectangle. It also reappears on the other side as if it emerged from a rectangular obscuration. This is what would be expected if the higher cognitive centers of the brain were interpreting the image(s) projected onto the cerebral cortex following the conformal transformation of the data received from the lateral geniculate nucleus. Anderson performed the same experiment for both vertical, horizontal and diagonal motions.

The analytical explanation for this phenomenon suggested by Anderson is worthy of further study.

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No effort was made to optimize the parameters of the transform or the angle of rotation. However, it is clear that the form of the parabolic transformation is appropriate. By adjusting the angle, $\theta$, and the width of the heavy line in the transformation, an excellent mathematical overlay of the data is available. The equation defines a finite magnification at the location of the point of fixation. Note the parabolic transform results in an open architecture. This architecture allows the field of view of an animal to be increased by expanding the radius of the occipital lobe (over evolutionary time scales).

The parabolic transform used, shown at upper left, is from a dictionary by Kober\(^{261}\) and the rotational procedure is presented in Roberts\(^{262}\). The hashed area in each figure of the transform pair represent the same area. The lines marked $q_1$ & $q_2$ represent horizontal lines displaced from the axis in the left transform pair. Tootell, et. al. noted the experimental difficulty of aligning the vertical meridian of the test target with the point of fixation. Fortunately, they found that the individual operculi mapped an area slightly beyond the vertical meridian. Thus, a finite width vertical bar centered on the point of fixation was mirrored completely in both halves of the striate cortex. More significantly, two separate copies of the area near the point of fixation in object space were formed within the striate cortex.

Yamamoto et al. have recently provided an analysis of what they describe as the retinotopic projection on the human visual cortex using fMRI\(^{263}\). Their clinical activity correlates well with the above discussion. They also introduce a number of new clinical techniques useful in diagnostics. They show that the foveola is not well represented in cortical space, disappearing off the representations at the left and right extremes.

It should be noted that while the community speaks casually of a retinotopic projection, this is not the precise case in this instance. Within about one degree of the line (and point) of fixation, object space is mapped linearly into a retinal image. At greater angles, the image of object space is no longer linear. It involves a trigonometric transform. The curvature of the right-most hatched lines in the Tootel figure (area farthest from the foveola) appear to highlight the presence of this additional transformation. In a truly retinotopic transformation, these lines (and the ones to their left) would be parabolic and concave to the left.

Data is available in Schwartz and elsewhere describing the mapping of the visual field onto the LGN and other visual areas but no information has been found mapping the visual field onto the PGN. It appears the mapping onto the LGN and the PGN are basically linear.

15.2.5.7.2 The cortical magnification factor in Macaque

Tootell, et. al. have provided the best available data on the cortical magnification factor, CMF, of monkey including a discussion of its uniformity among species of monkey\(^{264}\). The data is relative to object space and shows a systematic difference in CMF along the horizontal and vertical meridians of object space. It also clearly documents the parabola shaped representation of the vertical meridian in striate space. As a result of this feature, the local sign varies by nearly 150 degrees over the surface of the striate cortex. Because of this fact, it is possible to define virtually any global sign desired for this projection, depending on what integration area is used.


The data only applies to the central seven degrees of the field of view associated with the visual cortex. Within this region, the CMF varies along the two meridians (one of which is greatly curved) by a factor of five or six to one. The variation of the CMF outside of this small central region of the field of view is not addressed.

Using the mesh technique discussed in Section 15.1.2.3.4, and the transform equations of the previous section, it is possible to define the theoretical CMF for the Macaque quite precisely. The transformed mesh provides the local cortical magnification factor along each of the primary axes of object space at each point in striate space. By summing these two factors vectorially, a local vector is provided that exhibits both magnitude and angle. The angle of this vector relative to the stereotaxic axis defines the local sign at that point. The theoretical form provides a more precise interpretation of the CMF than defined to date empirically. Whereas Tootell, et. al. speak of a difference in CMF between the superior and inferior quadrants of the visual field, the theoretical CMF shows that the variation in magnification is continuous, varies significantly with position in the field, and depends on the rotation angle, θ. Only within a fraction of a degree of the point of fixation is the CMF remotely constant with angle in object space.

15.2.5.7.3 Retinotopic spread and acuity limits

Tootell, et. al. designed specific experiments to evaluate the resolution capability of the monkey based on the “Retinotopic” spread function (although there test configuration actually defined a spread function relative to object space). This is a minor point but is important from two aspects. The experiments focused on an eccentricity of 3°, well beyond the range of paraxial optics. At this point, the spread function of the physiological optics is significant in the overall performance of the eye. The spread function of the typical eye at 3°, derived from resolution tests, is considerably lower than for the foveal condition.

They found that the spread function at the striate cortex for the 3° eccentricity was about 2.2 minutes of arc in object space (140 microns in striate cortical space). While this may correspond approximately to the value of 1.5 minutes of arc given by Westheimer (1982), it is considerably below the limiting resolution of the human foveola which is less than 20 seconds of arc, based on either photoreceptor pixel size or tremor amplitude. Tootell, et. al. indicated the limiting spread function referred to the DG technique alone was about 100 microns at the half-amplitude points (pg 1505). Further development of the DG technique will be required to obtain a spread function size more indicative of the limiting resolution of the eye.

15.2.5.7.4 Mapping (conformal transformation) from object to striate space in humans

[xxx See also Section 15.6.5.3.5 for analysis of Tootell et al. work ]

The mapping of the external visual environment onto the human occipital lobe has been impeded by prior ideas dating from the “little green man” concept of a continuous retinotopic mapping across the longitudinal fissure. Only recently have texts begun to recognize the non-contiguous nature of this projection265. Baars discussed the significance of this splitting of the visual field and its ramifications266. In discussing the two distinctly separate projections onto the occipital lobes, he notes showing some consternation, “The most spectacular finding in that respect has been the discovery that the corpus callosum can be cut in humans, without changing the perceived unity of the world and of the self.” Recognizing the role of the pulvinar in foveal imaging, and the thalamus in assembling the final interpretation of the external visual field, provides a simple solution to this apparent difficulty. It also explains why a major cutting of the corpus callosum has so little effect. The large bidirectional commissure between the thalamus and the occipital lobes (Meyer’s loops) are not affected by such surgery.

In the 39th Edition of Gray’s Anatomy, the location of the two separate centroids of the visual field (the single point of fixation in object space) are shown as the left and right points of stereognosis. They are located behind the left and right ears respectively and not near a common point (or within the longitudinal fissure). The peripheral visual fields occupy the surfaces of the occipital lobe that fold into the longitudinal fissure as demonstrated by Harrington in his atlas. Harrington has even mapped the peripheral field showing the duplication of the vertical axis plus a margin in the two occipital lobes (page 125) of a patient with severe damage to the chiasm area. The visual sensitivity of the two temporal fields were totally lost but the nasal fields including the vertical axis and margins were retained. The patient was unaware of the loss of the two fields until age seventeen. The patient retained 20/20 vision within the area of macular sparing.

The locations of left and right stereognosis were inferred from the points of fixation on the cerebral cortex. The labels are appropriate for the centers of fixation in the two mappings but actually inappropriate for the centers of stereognosis. That process is actually carried out at high acuity in the pulvinar.

Harrington discusses macular sparing in the case of damage to the occipital lobes. He notes, “Macular sparing in homonymous hemianopsia is the rule in instaces of damae to the occipital cortex. Generally, it decreases in degree the more anterior the lesion producing the hemianopsia.” He also notes, “Much has been written and numerous theories have been proposed to explain the phenomenon.” However, these theories and discussions have not recognized the primary role of the pulvinar in evaluating imagery within the foveola. The region within a 0.5 degree radius of the fixation point is processed by the pulvinar at high acuity and in stereoscopy. The same region appears in only low resolution within the occipital lobe mapping. Recognizing this fact changes the parameters of the discussion of macular sparing.

Tootell, et. al. have recently created a high quality planar map of the human occipital lobe using MRI and computer programs based on the techniques of “formal” topography circa 1996. Figure 3 from that paper lacking discussion or the full caption of the original figure appears in Baars & Gage (page 69). It can be argued it is misleading. The original caption began with the word “apparent” and the text made it clear that the mapping included areas V1, V2, V3 and several others. However, the perspective of the mapping, shown in Figure 15.2.5-13, was chosen to highlight their exploration of V4 rather than illustrate the occipital lobe and V1. The chosen perspective does highlight the fact the point of fixation is not located centrally relative to the mapping onto V1 and suggests that V2 is actually the margin beyond the vertical axis passing through the point of fixation. Because of this rendition, Tootel et al. chose in their caption to describe the borders in frame C as “presumptive.”

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Tootel & Hadjikhani presented a more comprehensive analysis of the same data in 2001. The final analysis has

Figure 15.2.5-13 Tootell et al. projection of visual field onto the occipital lobe. Conventional posterior lateral views for human (A) and macaque (B). C; inflated posterior lateral view for human. The red bordered shading overlaying the solid colors shows variation among subjects due to gyri and sulci. D; inflated posterior lateral view for macaque. Note the unexpected location of the point of fixation (star) in C & D. From Tootell et al., 1996.
not yet appeared in an atlas form. The computer processing is extensive and significant. However, whether it is appropriate is yet to be determined. It makes a cut along the calcerine fissure beginning at the sylvan fissure and then flattens the two pieces of cortex above and below this cut. As a result, the horizontal axis is bifurcated at the sylvan fissure and the two sections of the vertical axis in the representation veer away from the horizontal axis rather than form a parabola about that axis. Any transformation of the spherical retina to a flat surface introduces significant distortions.

An alternate would be to keep the surface of V1 contiguous and make the cut along the margin just beyond the vertical axis as Tootell et al. did in their 1988 paper on the macaque. The vertical axis would then form a parabola about the preserved horizontal axis and circular sectors centered on the point of fixation become straight lines crossing the parabola. The margin to the right of the vertical axis would consist of a portion or all of V2. Otherwise, the point of fixation does not appear within the representation of V1 at all but only on its boundary. The suggested representation would maintain greater similarity to the macaque representation obtained by Tootel et al. in 1988 using radiographic techniques and demonstrate that the same parabolic conformal transformation was also appropriate for humans (possibly with different arguments). The caption for figure 2 of the Tootel et al. paper of 1996 noted, “The topography of human cortical areas is generally similar to that in macaques, except for an overall expansion; however, there are some noteworthy differences.” They went on to discuss the exceptions related to V3, V4v and MT, etc.). The caption concludes with an estimate of the linear and angular distortion due to flattening of about 15%.

A mapping based on this proposal is shown in Figure 15.2.5-14.
15.2.5.8 Important topological features of the Cerebellum

The cerebellum appears to be shared among a broad range of functional tasks within the nervous system. A region of the cerebellum known as the vermis appears to be dedicated to the visual function. This portion is located as near the thalamus as practical and probably communicates with it through the control point. Newell and Carpenter & Sutin (pg 455) appear to have different views of where the vermis is and how it is described. Newell shows the field found to be associated with vision by laceration and other faults or injuries. Other authors have indicated other portions also participate in vision. The functional role of the cerebellum stands between controversial and unknown in the current scientific literature. The role of the cerebellum has been difficult to define based on clinical observation because few subjects, agenic with respect to the cerebellum, survive postpartum. Those with a vestigial cerebellum are generally considered to be “slow to walk, to talk and probably remain very clumsy throughout their

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The control point described above could be defined as the hypothalamus based on morphology. It is known to support many other control type functions. However, most of these involve the neurosecretory system in conjunction with the pituitary gland. The hypothalamus appears to far from the thalamus and the cerebellar peduncles to play a role in the visual “control point.” The control point discussed in this work is more closely aligned with the thalamic reticular nucleus, TRN.

The functional complexity of the cerebellum is suggested by two facts. It is more highly folded than the cerebrum and, while physically smaller, has a total area equal to 75% of that of the cerebrum. In addition, it contains a large number of commissure that merely connect regions within itself. It is estimated to contain ten billion neurons. At the cellular level, as many as 300,000 axons may pass through the dendritic tree of each Purkinje cell, with as many as 120,000 participating in synapses. This is a clear indication of its many-to-few correlation capability in vision and its few-to-many translation capability with regard to skeletal-motor command expansion capability.

The most studied roles of the cerebellum have been those involving skeletal-motor circuits that are easily observed. While some areas are known to be related to vision, little is known about the functional aspects of that role.

15.3 The servomechanisms of the visual system of Chordata

This section will discuss the coarse and precision servo systems used to visually track objects by humans. These servo systems are able to track objects initially outside his field of view through inputs to the cortex from other sensors. Some of the lower chordates may also be able to track objects within their field of view without requiring a change in their line of fixation. It will be assumed that this process involves entirely computational techniques beyond the scope of this discussion.

Tracking of objects in extrapersonal space involves the entire sensory, computational and muscular capabilities of the animal. Thus the following material shares a base with a separate hotly debated discussion going on now in a broader field. “The prodigious output of the small army of researchers who have taken to summarizing the activity of motor-cortical units as a population vector in coordinates of polar extrapersonal space” has recently been reviewed, and criticized. Part of their problem has been defining the signal paths within the cortex that are relevant to their task. The description of the servomechanisms of the somewhat more constrained visual system contained here may aid this army. Hopefully, the information concerning the superior colliculus, the vestibular system, and the cerebellum, coordinated by the thalamic reticular nucleus, TRN, in this work will help them go beyond a model based on population based vector analysis.

The group of clinicians exploring the neurobiology of eye movements has been very active in recent years. One of the leaders in that field, Daroff, has recently provided a useful overview of the field as an introduction to a major volume of work. This volume was the record of a large scale symposium in 2001. Unfortunately, the terminology of most of this volume is heavily weighted toward clinical and medical usage. It differs significantly from that used here and in the academic vision community. Hopefully, the reader can perform a running translation by comparing the diagrams provided by each community. As Daroff points out, most of the clinical work has only achieved a precision on the order of minutes of arc. This level does not uncover the significant motions related to tremor which are fundamental to the understanding of the operation of the POS. There is also no discussion of the actual signaling within and between engines of the neural system, except with regard to recording the action potentials related to the Stage 3 projection system. It is hoped this volume will contribute to further understanding of the actual signaling.

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272 Loeb, G. & Brown, I. (1996) Directional motor control TINS vol. 19, no. 4, pg 137 attached to Konig, et. al. in my files xxx
Dell’Osso & Daroff have recently provided a series of conceptual circuit diagrams related to the precision optical system of man. It is hoped the drawings of this work expand on their drawings. This is particularly true in subdividing the various tasks among the different portions of the old brain and the neo-cortex and highlighting the key role of the TRN (shell surrounding much of the thalamus, see Section 15.6) acting as a gatekeeper. It is also true with regard to highlighting the closed loop nature of the Precision Optical Servo System or Precision Optical System, POS. This system only involves the old brain, except for certain volition commands accepted in incomplete (high-level) form from the cerebrum.

There are a few substantive differences between their drawings and this work. It is suggested that their figure 9-18 would be more useful with two changes. First, if the designation cortex was replaced by thalamus or divided into thalamus and superior colliculus. Second, if the putative efference copies of signals from the output of their three channels back to various inputs were eliminated. They are not required by the two-dimensional correlator of the PGN/pulvinar couple and the computational power of the superior colliculus. The inputs shown at the minus signs are not simple signals in the real case. They are outputs from the correlation process operating within the PGN in response to the changes in the image provided on the foveola in response to the angular rotation provided by the oculomotor muscles.

They recognized the critical nature of the tremor to the operation of the visual system but do not incorporate tremor into their diagrams. Their assumption that all neuron signals are positive (page 340) must be based on their conception of the neural system as relying upon action potentials for signal processing. Analog signals are used in the signal processing stages of the neurological system. Action potentials are only associated with the signal projections stages (the optic nerve and commissure).

Their introduction of a series of derivatives of various signals when discussing the dynamics of the oculomotor system should be recognized for what they are. The system does not employ differentiators as such. It does use differences in the amplitude of signals over fixed time intervals to compute differentials, but not true derivatives. The derivative symbol must be recognized as a convenient notational device representing a differential. Similarly, integrators appear to be implemented using short term memory and addition on a cyclic basis, relative to a sampling time interval, rather than true integration. Such integration (similar to that used in digital computers) is not subject to leakage of the type found in circuit element based integration and suggested on page 332.

Optican & Quaia have provided an article in the above volume. It contains many ideas compatible with this work. However, the article is essentially limited to the volition mode of operation of the saccadic system (including a veto capability over certain alarm commands from the LGN). It notes the superior colliculus is difficult to label either afferent (sensory oriented) or efferent (motor oriented). It concentrates on signals from the cerebrum commanding the vermis of the cerebellum directly instead of through a control point prior to the superior colliculus. While it introduces a pilot map to aid in controlling the saccades, it does not consider a partitioning of the retina into a map that can provide signals in retinotopic coordinates that can directly control the generation of oculomotor commands without significant computation of angles, etc. It does propose the superior colliculus contains a “target map” and the cerebellum contains a “pilot map.” These are conceptually similar to the proposal of this work. Carpenter & Sutin have contributed the fact that the volition commands generated in area 6αβ of the pre-motor area of the cerebrum result in much more coordinated motions of the oculomotor, head and skeletal portions of the body than do similar command issued by the motor area (area 4).

Figure 15.3.1-1, displays the Precision Optical Servo System or Precision Optical System, POS, of higher chordate
vision. A portion of this system, enclosed within the dotted box, has been known as the Auxiliary Optical System, AOS, or the auxiliary optical nucleus for a very long time because of its location near the initial optical centers of the brain. The lower part of the box, and including the 3 pairs of ganglion cells, is frequently labeled the oculomotor nuclei. The AOS and the associated ganglion cells are considered part of the lower or old brain. The morphology of the complete POS can be found in Pansky, et al\textsuperscript{278} although it is presented as a series of separate drawings.

The actual functional purpose of the Precision Optical System has not been described before in detail. Rodieck\textsuperscript{279} speaks of it as involved in the stabilization of the visual line of fixation. This work takes a fundamentally different view. Although one of its modes involves stabilization, its more important role is in the perturbation of that line of fixation as a tool of the perception and recognition functions. This system provides a unique starting point, at the block diagram level, for the discussion of perception using the specific definition of that term found above.

The POS employs a wide variety of very sophisticated signal manipulation techniques. Some will only become apparent during the following discussion. The primary feature to notice is the combination of analog (electrotonic) and pulse signal processing. On the ocular platform, the distinct nature of the various signals is well documented. Nearly all of the signal processing occurs in the analog domain until the ganglion cells are reached. This point of demarcation is shown by the diagonal hatched bar. The analog signals to the left of this point culminate in the input circuits of the ganglion cells. The output circuits of these same cells are represented by action potentials.

The signals from the luminance matrix are shown bifurcating after traveling over the optic nerve. This bifurcation is separate and distinct from that occurring in the optic chiasm in order to combine the signals from both eyes. This additional bifurcation separates the signals going to the PGN of the AOS from those going to the LGN. It appears that this bifurcation may employ branching of the fovea related

\textsuperscript{278}Pansky, B. allen, D. & Budd, G. (1988) Review of Neuroscience, 2\textsuperscript{nd} ed. NY: Macmillan, pp. 136-155

\textsuperscript{279}Rodieck, R. (1979) Op. Cit. pg. 204-206
Figure 15.3.1-1 The Precision Optical Servo System of chordate vision. It also includes the cognitive areas critical to the operation of both the coarse positioning system and the POS. The heavy lines indicate connections supporting Action Potentials. Only the servo loop operating in the vertical plane is shown in detail. The system employs sampled data servo techniques within a state variable servo loop to control the relative angle $\alpha$ within the scene under a variety of operating conditions.

neurons but merely a division in the routing of the other neurons. This figure highlights the importance of the 2nd lateral processing matrix in the pointing of the human eye. Although this matrix is not nearly as well developed in human as in some chordates, it is critical to the precision pointing performance of the eye. Whether signals from this matrix also bifurcate with some proceeding to the LGN is not known.

The signals from the 1st lateral processing matrix have been omitted from this figure. They are not believed to play any role in the precision pointing system of the human eye. This is confirmed casually by the well known difficulty of reading material printed in red with a green surround of the same luminance (Chapter 19 addresses Reading). More scientific investigations of this conclusion have been carried out with fish, insects, turtles, and primates. The recent work of Schaerer & Neumeyer is representative\textsuperscript{280}. Within the regime they were studying, they arrived at the general principle that motion detection did not involve the chromatic aspects of vision. Although beyond the scope of this work, a general reading of the literature supports the above conclusion.

The most important characteristics of the signals emanating from the luminance processing matrix, to the

\end{footnote}
positioning system of the eye, are the location of features in the field of view and their variation in luminance with time. These signals will be used in the threat evaluation and evasion system of the animal (since optimized by man for other functions as well). The primary response of this system is to instruct the eye to bring the line of fixation of the eye to the recognized location of the threat.

The most important signals emanating from the 2nd lateral processing matrix are difference signals between the luminance applied to various pairs of photoreceptors in the foveola. These signals are used in the AOS portion of the POS to support the perception and later recognition of the portion of the scene imaged on the foveola. In human, this matrix is not well developed. In this species, difference signals derived from either the LGN or Area 17 may be important.

Discuss PGN and projection neurons to other locations in the brain and those locations XXX.

Include the fact that the Purkinje cell found in the brain is a ganglion cell by another name. It is an encoder that produces action potentials for intra-cortex communications. See Nam & Hockberger\textsuperscript{281} Talk about question of spontaneity versus normal free running mode used in midget ganglion cells. Note Nam’s suggestion that dendrites are required for spontaneity.

To understand the complete system, it is necessary to appreciate the various states within which the plant, or physical part of the servo system, operates. Table 15.3.1-1 summarizes the most important of these states.

### TABLE 15.3.1-1
The Principle Operating States of Servo System of the Human Eye

<table>
<thead>
<tr>
<th>Function</th>
<th>Fixation</th>
<th>Perturbation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Activity</td>
<td>Saccades</td>
<td>Movement</td>
</tr>
<tr>
<td></td>
<td>Large</td>
<td>Small</td>
</tr>
<tr>
<td></td>
<td>Linear</td>
<td>Repetitive¹</td>
</tr>
<tr>
<td></td>
<td>Flicking</td>
<td>Tremor</td>
</tr>
<tr>
<td>Voluntary Mechanism</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Involuntary Mechanism</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>Alarm</td>
<td>Analysis</td>
</tr>
</tbody>
</table>

1 Also known as optikokinetik nystagmus
2 The voluntary activities are generally associated with the upper anterior brain
3 The involuntary fixation activities are generally associated with the upper posterior brain
4 The Perturbation activities are associated with the Precision Optical System

The various states in the above table occur at different times and have priorities attached to them. Most only occur during wakefulness. However, many of them are observed while the subject is sleeping. These operating states are generally occupied in the following sequence. When the subject is most relaxed, the tremor state insures the eye is functional and creating a static image from the input illumination falling upon the change detectors known as the photoreceptor cells. If an interest is taken in the image formed on the foveola, the eye will enter a repetitive sequence of flicking followed by tremor. This sequence will continue until one of two events occur. Either, the subjects interest will be drawn to a different part of the scene or a threatening situation will occur. Lacking a threat, the eye will switch into the saccadic mode to reorient the line of fixation to the new point of interest. A combination of large and small saccades will be used to reorient the line of fixation to the point of interest.

If the point of interest is moving continually at a relatively low rate, the eye may enter the continuous pursuit mode. This mode employs a virtually continuous series of small saccades interspersed with the flick and tremor modes. If the point is moving too fast, as the view close outside of a train window, the repetitive pursuit mode will be entered. This consists of a series of rapid small saccades followed by a large saccades to jump ahead inf the scene.

In the presence of a threat, perceived through any of the senses, the eye will be commanded by the involuntary portion of the posterior cortex via the sympathetic nervous system to reorient the line of fixation, and the head and/or body via the skeletal motor system if necessary (all in a coordinated manner), to bring the image of the threat into the foveola where it can be analyzed using the above modes.

The above modes are controlled by permanent memory, labeled PROM₁ in the figure. This PROM is primarily genetically encoded to be on alert for a variety of threats but can also be conditioned to new threats. This PROM also sets the priority for the above operating modes. Clearly, a threat to the animal takes precedence over all other visual activities until it has been perceived, recognized and appropriate action taken. The next level of precedence includes the voluntary saccadic movements. These movements will normally be followed by the analytical movements, flicking and tremor. Much of the above PROM may be morphologically situated in the cerebellum.
The flicking and tremor movements appear to be controlled by a simpler permanent memory element, labeled PROM2 in the figure. This PROM may be used to program the three terminal nuclei, the dorsal terminal nuclei, DTN, the lateral terminal nuclei, LTN, and the medial terminal nuclei, MTN or it may be used to control a separate and distinct waveform generating circuit such as the perturbation generator shown in the figure. These nuclei are either replicated or subdivided in order to provide control functions to both the twitch and non-twitch portions of the oculomotor muscles. The available information is presented in Buttner-Ennever, et. al282. They note, “Because the two sets of neurons do not receive the same afferents, they must have different functions; these are not yet clarified.” They also note, “These results are not compatible with the concept of a single final common pathway from motoneurons to eye muscles.” It is proposed here that the twitch channels control the tremor and the non-twitch channels control the larger saccades. Dimer has recently addressed the relative number of neural fibers associated with the twitch and non-twitch portion of the oculomotor neurons283.

The first paragraph of this Chapter stresses the vector nature of the afferent signals presented to the brain. This is important because many authors have sought to interpret the initial information provided to the brain in literal form. The brain does not receive an image map from the eyes that a human experimenter can recognize. This is especially true while the signals are in the highly compressed and encoded form in which they are transmitted over the Optic Nerve. Only after they are decoded and returned to analog form can they be effectively related to an image applied to the retina. At this point, the signals are no longer represented by action potentials! It appears that action potentials are only used within the brain when it is necessary to send information over relatively long distances. In this case, long distances might be considered a centimeter or more.

The Oculomotor nuclei of the eye are shown at the lower right. There are three structures previously identified through morphology; the dorsal terminal nuclei, DTN, the lateral terminal nuclei, LTN, and the medial terminal nuclei, MTN. Shown separately here, but probably included morphologically within these structures, are the pairs of ganglion cells associated with each nuclei and connecting to the respective muscles shown. Also likely to be located in the immediate vicinity is a perturbation generator used to provide flick and tremor commands to the individual nuclei. If located near these nuclei, there is no need for a signal projection circuit between the perturbation generator and the DTN and LTN. The three nuclei are shown connected directly to their respective ocular muscles via their respective ganglion pairs and through the labeled nerves as shown.

It is known that signals from the eyes to the CNS are suppressed during the repositioning of the line of sight by the ocular system (Section 15.3.5.1). The creation of the suppression signal (usually described as a blanking signal) is a logical task for the perturbation generator. Such a blanking signal is easily applied to both the LGN and PGN feature extraction engines. When applied to these two engines, all orthodromic engines will be prevented from receiving extraneous signals during large ocular rotations.

The diagram is partially generic in the lower area of the POS/AOS because, what is known of the required functional performance can be obtained using a variety of different detailed configurations. As an example, this figure represents the MTN and the oblique muscles of the eye as an error correction system to compensate for the lack of orthogonality between the dorsal and lateral muscle systems. Functioning in this way, the MTN does not receive signal directly from the other circuits connecting to the DTN and LTN. This subject will be addressed further in Section 15.3.2.

15.3.1 Complete and simplified servo diagram (except focus)

The servomechanisms incorporated into the visual system are probably the most complex in the human body. The overall servo loops implementing these servomechanisms employ a wide variety of individual techniques that are very sophisticated and have generally not been appreciated in the literature. Two critical areas that have not been

adequately addressed are the significant delays due to the very slow signal transport velocity in electrolytic conductors carrying action potentials, and the fact that nearly all signal manipulation within the neural system occurs in the analog domain. A third area not recognized in the literature is the presence of a complement to Meyer’s loop. This complement (Reyem’s loop) is produced by the variation in distance between different locations in the retina and their common exit point at the lamina cribosa. Each of these mechanisms, and many more must be understood if the overall servomechanisms are to be understood.

The following sections will present a series of simpler and simpler diagrams. The later diagrams will be seen to be complementary to those found in the recent literature. To simplify the presentation, the subject of maintaining focus will be treated separately in Section 15.3.3.

Figure 15.3.1-2 presents a simplified servo diagram applying to either the dorsal or lateral planes of the animal eye. Based on the underlying analysis leading to the figures for both the full and simplified servo systems of vision, it appears that the system controlling the oblique ocular muscles does not employ a separate servo loop of its own. The oblique ocular muscles are actually used to control a lack of orthogonality between the dorsal and medial muscle pairs. As a result, they act as a correction mechanism. The control signals for this correction system can be easily obtained from the dorsal terminal nuclei and the lateral terminal nuclei. These control signals could be quite easily obtained from the analog signals believed to be available within these nuclei.

The figure highlights some of the important functional features of the system. First the system involves two separate servo loops. The outer, coarse loop, is sensitive primarily to contrast changes at any given location in the total field of view of the retina. The inner, precision loop, is sensitive primarily to the location of specific contrast transitions, edges, in the field of view of the foveola. An initial question is how do these loops relate to common man-made servo loops? Normally, servo loops are defined in terms of an absolute quantity measured from some reference, using either linear or angular units. A type 0 servo loop corrects for an error in position, a type 1 loop corrects for an error in velocity, and a type 2 corrects for an error in acceleration. These types can be easily combined. The visual servo loops are more complex because of their multiple operating modes. A key feature of all of these modes is the presence of the input from the vestibular nucleus that provides the inertial reference for the system. Although an inertial platform is available to both servo loops, there primary operating mode is not sensitive to absolute position. They are primarily sensitive to the relative position of a feature within a scene given by the angle \( \alpha \) relative to the line of fixation. In this sense, both visual servos can be considered to have a mathematical term in the numerator of their transfer function that can be zero, e.g. the system has only limited capability of holding a given line of fixation in the absence of a feature in the scene selected by the cortex. The term in the numerator usually contains a time constant. In this case, the time constant relates to the time constant of the vestibular system and other propioceptors of the animal. This situation has significant medical consequences when circuit failures occur.

The outer, or command, loop follows the upper row of the figure to the magnocellular portion of the LGN and the cortex and returns in the lower right corner from the cortex. This loop can be considered closed in the conceptual sense but not in the definable hardware sense. It is closed via a mathematical calculation within the cortex. This command portion of the loop can only respond to the angle within the field of view unless additional sensory information is brought in from the other sensory organs. The second or inner loop is the precision optical servo system. When operating in the closed loop mode, it operates as a kind of type 0 servo loop. It can only correct for angular errors in the relative angle, \( \alpha \), measured in parts of a pixel projected into the object field. Rodieck has provided a conceptual servo loop for the eye and introduced, to the general biology population, the concept of an efference copy of the commands sent to the muscles of the eye that can be used as a pseudo signal to be used in the positioning servo loops of the eye. No need for such a concept has occurred in this analysis since the cortex

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receives a legitimate copy of the servo loop error signals as shown in both this figure and his variant.

Both the inner, precision, and the outer, coarse, servo loops employ pulse transmission techniques because of the length of the neural paths involved. Pulse transmission techniques are also widely used between major areas of the cortex because of the long neural pathways. The samplers used in these paths generate action potentials and are asynchronous. The sampler in the inner loop is also asymmetrical. The signal detector circuits are shown separated from the signal recovery circuits to emphasize their individual character. The feedback path from the state switch employ paired asynchronous samplers, signal recovery circuits, and actuators. The critical element in the system is the state switch. It determines the operating mode of the circuits at any instant and is basically under the control of the largely genetically programmed read only memory of the cortex, PROM, not shown.

[check the following paragraph]

Although both servo paths appear to use luminance channel information only (that is derived from the individual photoreceptor channels), they are significantly different. The asynchronous sampler in the Cortex path only processes monophasic signals and is of the typical parasol ganglion cell type. The asynchronous sampler in the inner loop involving the PGN processes biphasic signals and is of the typical midget ganglion cell type. The pulse train produced by this sampler is significantly asymmetrical with respect to the amplitude of the error signal. However, the dynamic range of the error signal, $\delta \alpha$, is quite small. There is no problem under normal operation.

Because of the limited dynamic range of the inner precision loop with respect to the angle, $\alpha$, this loop is incapable of tracking moving objects or determining the velocity of an object within the field of view. However, the outer loop is capable of recognizing the consistent error arising from the inner loop and thereby calculates an apparent velocity that it uses to generate a pursuit, or relative pursuit, command.
Figure 15.3.1-2 Simplified POS servo loop diagram illustrating the sampling devices and the state switch. The signal projection and association fibers are not shown in this figure.

It is important to note that, like other functions within the visual system, there are no bandwidth restricting or frequency selective filters within the servo loops of the visual process. The system is entirely direct coupled and uses a minimum number of circuit elements to accomplish its tasks.

The detailed operation of these two servo loops can best be understood by referring to Table 15.3.1-1.
15.3.1.1 The complete servomechanism subsystem of vision

Figure 15.3.1-3 presents the complete servomechanism (for only one of the two orthogonal systems of one eye) of the visual system in a single figure. The diagram is divided horizontally into three zones representing the eyes and related sensor systems, the old brain and the neo-cortex. At the lower left is the only mechanical portion of the system comprising the oculomotor subsystem and labeled “Plant.” The oculomotor muscles are shown in tandem and attached to the skull as its point of reference. The Precision Optical System, POS, and the Parietal-Occipital-Temporal lobe junction area, POT, are also shown in distinct groupings. Critical elements not shown in most similar drawings are the significant time delays shown throughout the system. These time delays are the reason for much of the morphological organization of the visual system. The location of the cerebellum immediately adjacent to the relevant portions of the mid-brain is not coincidental. This location avoids a significant delay for signals traveling from and to the PGN. It is critical to the rapid reflex actions of the system.

Another element not shown in most similar drawings is Reyem’s loop. This element is due to the variable distance between the various photoreceptors of the retina and the lamina cribosa. Because of the slow group velocity of action potentials traveling along these paths, there is a significant time dispersion introduced into the signals relative to their location on the retina. It is this dispersion that plays a critical role in the control of the vergence of the eyes in order to provide a stereoscopic view of object space. The time delays between the two related elements of a scene are compared in the LGN. Following the signal processing in the LGN, this time dispersion as a function of position is removed by the complementary Meyer’s loop. Within the LGN, an global (or average) difference in the time delays for all elements of the scene is calculated and transmitted to the PGN for use by the POS in adjusting the pointing of the eyes to cause a merged image at the input to area 17 of the cortex. The LGN also incorporates a vector component in the signals sent to area 17 representing the local difference in time delays of scene elements after subtraction of the global average. This component provides the stereoscopic information concerning the location in depth of a scene element with respect to the average scene.

When discussing the precise roles of some areas of the brain, it is difficult to be completely specific because of the wide variation in terminology used by different schools of investigation. The reader should allow some latitude in this terminology (such as whether area 39 should be used instead of area 7 when discussing where certain functional tasks are morphologically located within the POT) and expect additions and modifications to appear in the future.

The thalamus plays a key role in the overall operation of the visual system. The portion of the thalamus known as the TRN operates as a central switchboard for a variety of signals and also acts as a gatekeeper with respect to many signals with a potential for transmission to the Ocular Nuclei. Of greater importance, at least in humans, is its role in the precise analysis of the information presented to it by the foveola. The PGN/pulvinar couple is the key element in our ability to read abstract symbols. The dashed diagonal line highlights the major division of labor within the thalamus. Above the line are analytic and correlation activities. Below the line are the gatekeeper functions critical to controlling which signals from the cerebellum, and the Superior Colliculus are passed on to the Oculomotor subsystem. The diagram shows signals from the Superior Colliculus passing through the TRN. The morphological evidence would suggest the physical situation is better represented by the gatekeeper signals from the TRN being transmitted to a gate control mechanism physically located within the Superior Colliculus. The same architecture may be used to control signals from the cerebellum. There is very limited experimental data on the time sequence of visual signals as they pass through the visual system. Only with the recent introduction of the fMRI and VEP experiments using a strong local magnetic field as a probe have such information begun to appear. The information from these sources is still relatively gross. Some very detailed information concerning anatomic correlates with the organization of some of the proposed servomechanism components has been presented by Wirtschafter & Weingarden. However, as discussed herein, their hypothetical scheme for the servomechanism of vision is not supported. Their description of the pontine paramedian reticular formation (PPRF)
appears to relate to the previously described ocular nuclei of the POS.

The POT plays a key role in the cognitive portion of the overall visual system. Note that it is isolated from virtually all of its associated areas by finite delays measured in milliseconds. These delays separate its functions from the most rapid possible reflex actions associated with the cerebellum. The peduncle of the cerebellum is located immediately adjacent to the Superior Colliculus.

The overall operation of the servomechanisms of the visual system are most easily discussed in terms of the various signal paths labeled in the figure. There is a key division of these paths into two groups, those associated with alarm and awareness and those associated with detailed analytical functions. While these functions merge in the cortical areas of the brain, they are functionally separate in the mechanical performance of the oculomotor system. The separation is most easily recognized by the difference in spatial frequency response of the twitch and tonal segments of each oculomotor muscle. This functional separation allows the diagram to be divided into two separate diagrams using the rules for superposition of networks and will be used in the following sections. This separation is in general agreement with a theme in the literature that a change in object space within the field of the fovea will not cause a saccade. Such a change is processed within the elements of the analytical path.
A nucleus known as the oculomotor ganglion, has been identified morphologically in the neural path (signal circuit) extending from the oculomotor nucleus to the muscles of the eyes. Its purpose has not been defined in the literature. Based strictly on the architecture of the above figure and the magnitude of the delays shown, it is likely that this ganglion is provided to allow an alarm mode signal to be introduced into the oculomotor system with minimum possible delay. Such an override signal is likely to originate somewhere near the control point (the thalamic reticular nucleus) and go around the significant delay associated with the oculomotor nuclei. This signal path is indicated by the heavy arrow in the lower left of the figure.

Subsequent to the preparation of the above figure, figure 15.11 of Schall was found. These figures are practically overlays of each other. Schall specifically illustrates the dual paths (awareness path and analytical path) leading to the Inferior Parietal Lobe (Area 7) defined in this work. All of the paths defined here can be highlighted in the Schall figure (except for the alarm path from the LGN to the Pulvinar/Central thalamus). Schall was presenting a review and relied upon inputs from many experimenters and clinical observers. He shows many reciprocal paths between two neural engines. His figure does not develop the signal delay between the various engines and elements. It is proposed that many of these (conceptual) paths would disappear if his sources had collected their data at a time resolution better than about 3 milliseconds. It is also suggested that his grouping of many functional elements under the designation Cerebellum does not recognize the command authority of the combined Pulvinar/Central thalamus shown in his figure over many of these individual elements. Expansion of his figure in this area would allow the reflex path to be shown more distinctly.

In the same publication as Schall, Stein & Meredith (page 86) discuss the dual nature of the visual signaling system. They suggest that one system concentrates on awareness (visual attention and orientation) and the other on analysis (of object features such as pattern).

The dashed box in the above figure includes the neural elements associated with the analytical path. The level of development of the elements within the box are highly indicative of the level of the animal within the phylogenetic tree. These elements are critical to the analytical capability of the animal. They are crucial to the interpretation of fine detail and symbols (such as those found in writing). It is most highly developed in man and the other great apes. Its level of development is significantly lower in the lesser apes and other chordates. This fact is crucially important when attempting to relate the visual performance of other animals with that of humans. The analytical and oculomotor subsystems of cats and monkeys are significantly different than those of man. This fact must be recognized in laboratory investigations and subsequent published papers.

15.3.1.2 Comparisons with the literature

After exploring the definitions of vision and blindness (as also discussed in Section 18.1.2), Schneider described two visual systems in the Syrian golden hamster. His performance based results clearly support the description of the awareness, analytical and alarm modes of the above figure. The work is notable in its confirmation of an analytical mode in the hamster as well as the human (and therefore probably all—at least warm blooded—chordates). His analysis alone would support a separation between the foveola and peripheral paths from the retina to the brain.

15.3.1.3 The low frequency servomechanism of vision—pointing

The low frequency operation of the visual servosystem is that most similar to the literature. It provides the steering commonly associated with the line of fixation of the eyes. Figure 15.3.1-4 highlights these functions. The low frequency portion of the servosystem has two primary functions, to maintain the visual portion of the cortical saliency map and to process the response to threatening changes in the environment surrounding the animal. Although these alarms can come from any of the sensory subsystems, they are most often from the auditory or visual

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subsystems. These alarms are initially received by the TRN and given a preliminary evaluation. If a single alarm is received, the response is directed to the cerebellum where a reflexive response is prepared and returned to the control portion of the thalamus for implementation. In the absence of any more recent change in the environment, this response is passed to the Ocular nuclei, and other skeletal motor control nuclei, for implementation. If a more complex multi-alarm environment is detected by the TRN of the thalamus, it may also pass the information to the POT for further, and simultaneous, evaluation. The POT may access the cortical saliency map if appropriate before preparing its recommended response and returning that information along the command path. Under this condition, the control portion of the thalamus compares the responses from the cerebellum and the POT and decides which action to implement. The awareness path is used continually to update the cortical saliency map via the cognition path.

The figure also illustrates the volition path over which commands generated in the higher cortical areas such as the frontal eye fields, FEF, are passed to the POT for implementation via the command path.
Notice the increasing loop delay involved in these alternate pathways. The single alarm is processed the most rapidly, employing only the thalamus and the superior colliculus. Any more complex situation requires significantly more delay in processing. In general, the overall delay is dominated by the limited response of the tonal muscles.

It is important to note that this diagram does not employ a “neural integrator” such as appears in many conceptual and hypothetical low frequency servo diagrams. This function is actually not performed in the neural system but in the oculomotor plant. It is associated with the tonal muscle as shown in the lower left of the figure. The neural system issues a group or burst of pulses sized to obtain the desired change in the angle of the line of fixation. These pulses are integrated by the muscle during its response.

It is also important to note that this diagram does not incorporate an “efferescent copy” of the muscle response or any proprioceptors. The error signal required by the servomechanism is produced within the retina itself as it records the location of the threat within the visual field as a function of location relative to the line of fixation and time.

15.3.1.4 The high frequency servomechanism of vision–analysis

The high frequency operation of the visual servosystem has not been discussed in detail in the literature. It provides the critical analytical function so important to humans and probably other higher chordates. Without this function, detailed analysis of elements of a scene, and particularly of symbols, is impossible. Figure 15.3.1-5 shows the critical elements of this portion of the system. This portion is not directly concerned with the general environment surrounding the animal. It is designed to analyze only the information in or very near the foveola. It only employs the very high frequency or twitch capability of the oculomotor muscles. This capability does not employ a significant integration function as does the low frequency component. The muscle motion is a direct reflection of the scan pulses it receives from the ocular nuclei. The PGN/pulvinar couple operates as a phase detector within a sampled data servo loop. It produces several outputs. The first output is the signal required to keep the servo loop in lock. This signal closes only the local position mode of the loop since the twitch muscles are not able to provide a significant change in, or maintain the gross angle of, the line of fixation. The second output is the schedule of microsaccades and minisaccades/flicks required to analyze the image presented to the 23,000 photoreceptors of the foveola.

This work assumes that the schedule of saccades is prepared within the thalamus based on previous training and its own short term memory. This assumption is subject to verification. The preparation of the schedule may involve either the cerebellum or the POT with their larger pretrained memory components. Under the baseline assumption, the thalamus generates a series of commands to the ocular nuclei associated with each of the planes of scanning motion that are designed to probe the character of the information within the field of the foveola as discussed in Sections 7.3 through 7.5. These motions relate to the tremor explored by Yarbus, Ditchburn, Shakhnovich and others.

As a result of implementing the schedule of saccades, the PGN/pulvinar couple is able to generate an additional output that is a vectorial representation of the individual elements of the image projected onto the foveola. This information is passed to the POT for interpretation and final perception. The POT does this in conjunction with the cortical saliency map which is its basic source of both historical and current information. The historical information includes that due to training.

If the thalamus is not able to produce the schedule of saccades internally, then it is suggested that this function involves the POT. In this case, signals are passed to the POT via the analytical path and the required schedule of saccades is passed back to the thalamus over the command path for implementation. Note the additional and significant delay introduced by this option. This option does not appear viable based on the known peak frequency of the microsaccades associated with tremor. The two delays shown between the eyes and the PGN are sufficient to limit the frequency response of this system to about 160 Hz in humans.
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Figure 15.3.1-5 The high frequency portion of the visual servomechanism crucial to the recognition of fine detail and abstract symbols.

15.3.2 Operating modes of the servo loops

The two state switches shown in the simplified servo diagram control the operation of the system. The system operates in a sequence of modes in support of the states defined in Table 15.2.2-1.

15.3.2.1 Basic mode of the coarse servo loop in higher chordates

In the most basic mode, the outer servo loop waits for a signal indicating a change in the illumination of at least one of the photoreceptors in the retina. Upon the receipt of this signal from the luminance processing matrix, the cortex first determines if this change is expected and routine (see the next Section). If so, it ignores it. If it represents a new situation, the cortex determines the distance of the affected photoreceptor(s), in two rectilinear coordinates related to the dorsal and lateral planes of the animal, from the fixation point of the retina. The cortex commands the actuator portion of the servo loop to change the line of fixation so as to bring the image point related to the change in illumination to the center of the foveola. This action may result in a large or small saccades. If it involves a saccades of longer duration that the perception time of the cortex, the upper state switch may open the circuit of the outer servo loop to prevent useless information being transmitted to the cortex. If the duration of the saccades is long enough to impact the adaptation state of the photoreceptors, a further command may be given to close the eyelid temporarily. The eyelid is not opaque but it does attenuate and average the light level during this interval. This servo loop then returns to its quiescent activity of waiting for another change in the illumination pattern of the scene.
The fact that the coarse servo loop is not a conventional analog loop is emphasized by the commands issued by the cortex. In an analog mode, the muscles would react in proportion to the magnitude of the error signal and the eyes would rotate in an approximately sinusoidal manner. This is not the case in chordate vision. The cortex issues a command to start the rotation of the eye (at high speed) and a second command to stop the rotation. The eye itself accelerates rapidly to a maximum rotational speed and then continues to rotate ballistically (at a nearly constant speed) until it is commanded, after a computed interval, to stop. This mode of operation raises the performance capability of the eye considerably.

After being alerted to a threat, the cortex appears to use signals from the 2nd lateral processing matrix to determine how to instruct the ocular muscles in order to bring the image of the threat into the foveola. The appropriate signals are the two orthogonal “zone difference” signals discussed earlier. These signals are fundamentally analog bi-phase difference signals. They may be created in bipolar cells or in specially modified midget ganglion cells capable of receiving signals at both their dendritic and poditic inputs. These bi-phase outputs describe the location of the threat in the retinal field. One relates to the lateral position and the other relates to the dorsal position relative to the retina. These bi-phase signals are used, in separate midget ganglion cells, to generate two streams of action potential streams. Since action potentials generated from bi-phase signals are asymmetrical, it is expected that the speed of response of the cortex will be different for threats located on opposite sides of the fovea. This consequence has been observed and reported by Oyster289. He says the rabbit eye responds faster to changes (he only discusses movement) in the anterior portion than in the posterior portion of the field of view. He gives an alternate cause for the difference. The alternative is based on the number of global direction-selective units in various regions of the retinal system instead of a single pair of “zone difference” signals from only a few distinct midget ganglion cells. He also says the magnitude of the optokinetic response is larger for changes affecting the peripheral retina than for the central retina. It is not clear if he was referring to the total time required to react or the maximum velocity of ocular motion.

Van sluyters, et. al290. have provided an excellent review of the AOS, using the notation NOT for part of it, in the neonate and adult human and several other species. It concentrates on the optokinetic reflex (OKR) rather than the entire array of responses of the AOS. There is a problem with the term optokinetic reflex. It is too restrictive. In the literature, its action is usually restricted to a stabilization of the line of sight. In fact, the optokinetic response of the eye is controlled by a variety of signals, some of which are voluntary and even based on abstract thought. These responses do not involve a reflex. Other signals impacting this response involve auditory signals. The response may call for rotation of the eye, head and body to positions beyond the initial field of view of the eye. The more general term optokinetic response would appear to be preferable. OKR will be used in this sense in the remainder of this document.

Figure 19 of van Sluyters, et. al., drawn from Hoffmann291, can be expanded into the variant shown in Figure 15.3.1-6

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289Oyster, C. (1968) The analysis of image motion by the rabbit retina. J. Physiol. vol. 199, pg. 613-635--see also the 1972 article, same publication, pg. 184 for a correction.
15.3.2.2 Response of the ocular muscle system

Oyster has provided comprehensive data on the ocular motions of rabbit in response to stimuli. However, even experimenting with 762 neural units in 31 animals, the standard deviations associated with any individual parameter is still on the order of 6-12 degrees. The experiments used electrophysiological probing of ganglia in the retina to determine their receptive field of view and sensitivity to the motion of a spot of light. The result was a classification of cells based on the nature of their action potential stream. His discussion of the musculature of the animal is less comprehensive than that of others. Oyster basically dismisses the importance of the oblique muscles as “muscles of pure torsion, and thus do not contribute significantly to movement of the visual axis.” Similarly, he describes the rectus muscles as contributing little or no torsional component to the motions of the eye. The precision desired here requires a more careful examination of the torsional contribution of these muscles. Other investigators have found that the attachment points of the rectus muscles in human contribute up to about four degrees of rotation of the line of fixation and this is enough to cause problems in image registration in the cortex. This problem is particularly (doubly) severe in binocular vision due to the counter rotation between the two eyes when they converge. The oblique muscles are specifically tasked with eliminating this rotation. Based on this interpretation, the axes of Oyster that are based on a static morphological examination should be modified to agree with the dynamic situation. It is the correction provided by the oblique muscles, driven by the medial terminal nuclei, that create the dynamic axes in the rabbit--as well as other chordate animals. These dynamic axes of rabbit appear to be rotated approximately five degrees from the static axes determined by morphological dissection. With this modification to the operating concept of the eye, Figure 15.3.1-7 presents the data of Oyster adapted to the new axes. Note that the correction required of the two muscle pairs is different due to the different connection points of the muscles to the ocular globe. The medial terminal nuclei can support this differentiation. In chordates with more distinct forward vision, the posterior and anterior rectus muscles are renamed the lateral and medial rectus muscles respectively. The angular impact of the oblique muscles, and their instructions from the cortex may change with the degree of forward vision.

Figure 15.3.1-6 Simplified servo loop of vision. Compare to Hoffmann (1987)

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In this work, a very few ganglion cells are required to control changes in the line of fixation of any eye. These few cells may not have been found in Oyster’s studies. To avoid requiring calculations involving trigonometry in the cortex, it is proposed that these ganglion cells receive inputs from bands of photoreceptor cells in the retina that are perpendicular to the direction of rotation caused by the ocular muscles. These bands would be arranged in two orthogonal sets. The bands could be so narrow that they can be represented by a gradient. The cortex would evaluate how far any stimulated photoreceptor was from the fovea by its position within these two orthogonal “band” structures. This distance would then be used to control the ballistic motion of the ocular globe in the two directions. The medial terminal nucleus would calculate the instructions to the oblique muscles to insure orthogonality between the two planes of ocular motion and no rotation of the line of sight.

When the effect of the oblique muscles is included, there appears to be no need to introduce the 10.7 degree rotation suggested in figure 3 of Oyster.

**15.3.2.3 Augmentation of the Basic mode**

In the basic mode, the eye acts only as a change detector. The animal is essentially blind and only able to see changes in its field of view. This situation was well explored by Yarbus. In the higher chordates at least, an additional signal has been introduced into the coarse servo loop. This is the tremor signal produced by the perturbation generator and delivered to the line of fixation generator. This signal causes the muscles of the eye to continually shake the ocular globe through an angle approximately equal to the angular subtense of one photoreceptor cell. This action results in a the generation of a low-level signal indicative of a change in illumination by nearly every photoreceptor cell in the eye within a single perception interval of the cortex. The cortex uses this information in two ways. It initially uses it to form a complete image of the visual environment defined by the instantaneous field of view of the eyes. If necessary, it commands the actuators to slew the eyes in order to obtain information on the total visual environment. If necessary, it will also cause the head or body to rotate in order to complete this survey. After obtaining this initial visual map in vector form, the cortex will hold this map in short term memory. It can then use this map in its evaluation of the importance of any more significant changes in subsequent luminance signals. This evaluation discards at least 90% of the data arriving from the retina on a per perception interval basis.

The tremor signal is the fundamental mechanism for converting the chordate eye from a change detection system into an imaging system. The tremor signal results in a very low level but continual motion of the eye. This motion is usually described in terms of a pseudo random waveform with an amplitude of nominally 20-40 arc seconds amplitude in object space and a bandwidth of 30-90 Hz.

**15.3.2.4 Basic mode of the precision servo loop**

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The precision optical servo loop, becomes active after the coarse servo loop has caused an area of concern (interest) in the visual field to be moved to the point of fixation within the foveola. The precision servo loop performs the perceptual task prior to transmitting vector information to the cortex for recognition and further cognition. This loop takes its input from the 2nd lateral processing matrix. Thus, the signal is basically a difference signal representing the change in contrast sensed by individual photoreceptors of the foveola as the image moves quickly over it in response to the tremor signal. It only requires a few perception intervals for this perception to be accomplished since the foveola is itself a two dimensional array of cells operating in parallel. If the image of interest is complex and of finite size relative to the photoreceptors, this fact is reported to the cortex and an additional capability is invoked.

The cortex instructs the perturbation generator to produce flicking signals that are used to modify the line of fixation incrementally. This allows the foveola to analyze larger features. The resulting overall scanning pattern has been widely reproduced based on the early work of Yarbus. Figure 15.3.1-8 reproduces the famous young girl picture from figure 114 of Yarbus. More recent papers by Ditchburn and Skavenski, et. al. have added more detail to this literature. Very recently, Tatler et al. have presented more of Yarbus’s data. Yarbus and Ditchburn used the technology available to them at the time to measure the fine movements of the eye. This basically included a bite bar (that should be mounted on an inertial mass), to attempt to immobilize the movements of the head to the level of a few arc seconds or better, and a small mirror, acting as a galvanometer that recorded on photographic paper. This method allowed a very precise characterization of the tremor. It was found to have an amplitude of 20-40 arc seconds and a frequency spectrum extending to 70-90 Hz.

Skavenski, et. al. had new technology available and went further. They were able to instrument both the head and eyes separately. However, the ultimate sensitivity of the magnetic pickup technique they used appears to show less accuracy than the optical techniques of Yarbus and Ditchburn. They did separate the fine motions of the eye from the undesired but prevalent fine motions of the body, but only at an accuracy in the fractions of a degree and only in a few of the six degrees of freedom involved. Figure 15.3.1-9 presents some of the data of Skavenski, et. al. For a subject attempting to fixate on a point in space. (Need skavenski paper. Rodieck appears to pollute the data by introducing the eye chart. He then jumps to stabilization instead of perception.)

Both Yarbus and Ditchburn noted the character of the flicking motion. It is also appears as a pseudo-random process overall but is in fact a very complex process under cognitive control. Its maximum amplitude is typically larger than that of tremor but its frequency is typically lower. The sum of the flicking and tremor frequency spectrums resemble a 1/f frequency spectrum. However, this is misleading, the observed signals are not random. Only very sophisticated instrumentation can characterize these signals further, and individually.

The necessity of isolating the fine motions of the head and body from the eye during normal operation of the

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precision servo loop is achieved by using signals from the vestibular nucleus.

Whereas an asymmetrical sampler is employed in the signal projection portion of the servo loop, this is of little consequence because of the small signal perturbations found inside the loop. In the muscle actuating portion of the system, similar asymmetrical samplers are used in the signal projection system. However, a pair of signals is transmitted as shown. The two members operate in what is normally labeled push-pull configuration. And, because of the ballistic mode of operating each pair of muscles, any non-linearities in the operation of these circuits are of no importance.

The combination of the tremor signal and the flick signal are key to the generation of perception information by the precision servo loop. This information, when passed on to the cortex, is critical to the sophisticated recognition function resulting in the humans ability to “read” characters and recognize other fine image detail.

15.3.2.5 Performance of the servo loops of the human eye

There is a great deal of psychophysical data on the pointing capability of the human eye accumulated under a wide variety of conditions and using many methods.

15.3.2.6 Summary of servo loop operation

Further delineation of the modes of these servo loops is not warranted here. Much more data can be extracted from the literature. Much better instrumentation can be employed based on new test designs using the servo loop characteristics presented above.

15.3.3 The auxiliary servomechanisms of vision (RESERVED)

15.3.3.1 The servomechanisms controlling the shutter (eyelid) (RESERVED)

15.3.3.2 The servomechanism controlling focus and vergence (RESERVED)

[XXX This section is currently in development ]

The configuration of the physiological optics of humans are discussed in Section 2.4.2.3. Some aspects of the operation of the optics related to accommodation are reviewed in Section 17.7.2. This section will review the servomechanism acting upon the optics and providing this accommodation.

As in the previous sections, the top level schematic diagram first presented in Section 15.7 can be simplified to focus on the automatic focus control and vergence control servomechanisms. The appropriate simplification is shown in Figure 15.3.1-10. [xxx show efferent nerve number and note it passes up the optic nerve. show lens and actuators EXPAND to show vergence action on oculomotor muscles.]
Although not discussed further in this section, it is quite likely that the servomechanisms related to vergence and focus depend on stored information to allow them to respond a priori to an instruction from either the stereo mode or the volition mode signal paths. This situation would suggest that the appropriate vergence and focus instructions are part of the complete command vector issued by the TRN and/or processed by the superior colliculus. If correct, this interpretation would suggest that the detailed commands provided to the oculomotor neuron nuclei are based on a PROM. This situation would, in turn, suggest that the original command instructions are learned initially. This would support to use of bold edges in the decorations in the room of a baby.

**Figure 15.3.1-10** Simplified top level schematic of the focus servomechanism. The signals to control the lens muscle are derived from the raw spectral channel information by the PGN/pulvinar couple. The drive signal at “B” is probably formed in the Superior Colliculus based on a signal provided from that couple. The channel is probably similar to but independent of the three nodules shown.

15.3.3.2.1 The operation of the vergence servomechanism of vision

As discussed in Section 15.7.7, the acquisition of a vergence error signal is a primary responsibility of the thalamus. It is likely that a coarse signal is provided by the LGN’s and a more precise signal is provided by the PGN’s. The required signals are easily obtained from the data provided to the individual pairs of layers in the LGN. The best data would be obtained from the magnocellular layers because of their finer time resolution. As shown in the figure caricaturizing the signals in the LGN and PGN, any time delay between the appearance of a signal due to a particular object in the scene in the retinotopic map of one eye versus the other is a direct measure of the vergence error between the two eyes. This difference in time can be measured using a “box car” circuit. Such a circuit provides an
output pulse with a duration directly proportional to the error. Such a signal is easily obtained by applying the signal from one pixel of one eye to the dendritic input to a neuron and the signal from the same pixel in the other eye to the poditic input. The output will consist of a box car pulse. To obtain an average error over a region, the signals from a region of pixels in one eye can be applied to one dendrite and the similar signals from the other eye to the poditic terminal of only one neuron. With appropriate biasing, the output will have a duration equal to the average error for that region.

By averaging this error over a significant part of the binocular field of view, a signal is derived by each LGN that is directly proportional to the error. This signal can be provided to the TRN for incorporation into the vector describing that scene. Since it will normally receive two inputs, the TRN must process the information further to obtain a nominal correction signal. It is this signal that can be used by the POS to converge the eyes properly.

The above description of the signals and responses of the vergence servomechanism is very similar to current pointing servomechanisms used in man-made aircraft and gunnery systems.

**15.3.3.2.2 The operation of the focus servomechanism of vision** (RESERVED)

[xxx This section is under development. refer to figure 15.3-2 as a simile and show a figure like figure 15.3-3 in figure 15.3-11. No need for high frequency plant. Comment of speed of focus if any data is available.]

The ideal relaxed eye would be focused at infinity. Under this condition, the anterior surface of the lens would have a nominal radius of 10 mm. When commanded to focus on objects at close range, the curvature of this surface changes to a nominal radius of 6 mm.

As shown in Figure 15.3.1-11, the lens servomechanism can be modeled as a spring loaded mass that can be acted upon by the lens muscle to move the location of the Petzval Surface of the optical system into coincidence with the nominal focal plane of the retina (at or near the point of fixation). Since the location of the Petzval Surface would move with the distance to the object of interest along the line of fixation, it is the job of the focus servomechanism to change the optical power of the lens to compensate for this motion.

The only information available to the POS with which to obtain information about the object of interest, is the signals from the photoreceptors of the foveola. There is limited data available on how the circuits of the old brain process this information to extract the necessary focus adjustment signal.

The available evidence suggests the focus signal is extracted primarily, if not exclusively, from the luminance channel signals. This conclusion is supported by the difficulty in reading a highly colored but equal luminance type face. If chrominance information was used, it would pass through the channel broken by the question mark in the figure.

It is clear that the POS maintains a nominal output signal until it detects a change in the quality of the focus. Only when sensing the need for a change does the servomechanism respond.

A good example of this is trying to find a small airplane against a nominally clear sky. Unless one makes a special effort to focus the eye to infinity, it will remain focused at a more finite distance and it becomes very difficult to find the aircraft. If the eye can be relaxed, or focused for an instant on some other very distant object, the airplane immediately becomes visible.

**15.3.3.2.3 Effect of aging on the focus servomechanism**

The principle impact on the automatic focus servomechanism of aging involves the lens and its actuating muscle. The primary change is believed to be a loss of elasticity in the lens. This loss causes its spring constant to become
larger. This change requires greater force to distort the lens by a given amount. It appears that the lens muscle is not able to grow or otherwise increase its operating capability to meet this demand. As a result, the range of focus of the eye becomes less and less with age. The average location of this reduced range of focus tends to approach infinity (one typically needs longer arms to read).

15.3.3.2.4 Errors associated with the focus servomechanism

As noted in Section 17.7.2.1, there are a number of clinical diseases associated with failures in the automatic focus system. They are generally classed under the clinical title myopia. However, they include a broader range of conditions involving hypo- and hyper-metropia. Some of these are correctable with external optics (refractive myopia). Others are neurological in origin (neurological myopia). Refractive myopia will not be addressed here.

Neurological myopia involves a failure in the circuits of the focus servomechanism. Insufficient experimental data is available to pinpoint the specific errors. However, based on the similarity to other errors associated with color blindness, and particularly the complex clinical syndrome known as achromatopsia which includes the syndrome of myopia, a probable cause can be given. The error is probably due to an error in the impedance associated with the electrostenolytic process providing power to one or more of the individual circuits within the thalamus, the superior colliculus or the neural path connecting them. There are two potential errors associated with this error mechanism. The gain of one of the analog circuits could be reduced. Alternately the quiescent voltage level of one of these analog circuits could be offset from normal. An offset would introduce a permanent error in the positioning of the Petzval surface relative to the fovea (irrespective of the use of external corrective optics). Inadequate amplifier gain on the other hand would reduce the precision achieved by the servomechanism. This result would reduce the normal neurological acuity of the eye in the direction of the more definitive condition associated with clinical amblyopia shown in [Figure 17.7.2-1].

15.3.4 The POS as controller of the servo loops

As suggested above, it appears the motion of the eyes is controlled using a variety of stored instructions that are reflexive in nature and largely learned. These instructions appear to be stored in short, medium and long term memory as appropriate. Oyster has provided several simple block diagrams of the POS in a less refined form298. He has not differentiated between the twitch and tonal neural channels and relies upon the concept of a physical neural feedback path (the efference signal) that does not appear to play a significant role in the actual visual system.

The literature has not completely identified the signals carried by nerves number III, IV and VI. The fact that two distinct nerves, III and VI, are described as supporting each of the medial and lateral rectus suggest that the same situation may apply to the superior and inferior rectus muscles. It also suggests that these nerves serve the twitch and tonic portions of these muscles separately. This situation would also support the separation of the servosystem into high and low frequency portions. As a result, one pair of nerves would originate in one area of the old brain and serve the high frequency portion and a second pair of nerves would originate in a second area and serve the low frequency portion. The nerves supporting the low frequency portion would be expected to originate in the superior colliculus area and be closely associated with the command signal path. The nerves supporting the high frequency portion would be expected to originate in or near the PGN and be more closely associated with the analytical signal path.

In both of these situations, the pulses transmitted to the oculomotor muscles over these nerves are action potentials. However, the interpulse spacing of these pulses would be tailored to meet the performance requirements of the analytical and command signal paths. In general, the signals to the muscles of the low frequency portion would consist of strings of pulses designed to cause major saccades and to maintain a given eccentricity when required. In

the case of major saccades, the strings would be closely spaced groups that would effectively overdrive the muscles as so frequently described in the literature. These pulse strings would be applied to one muscle of a pair to start the saccade and to its complementary partner to stop the saccade. The result would be a bang-bang mode of operation with the velocity of the eyes being parabolic in form (but not technically ballistic because of the finite duration of the pulse strings employed). This mode is used by both the vertical and horizontal pairs of muscles. The oblique pair also uses this mode of operation. However, the pulse string is structured slightly differently in order to provide a correction to the motion instigated by the other pairs.

To maintain a given eccentricity, more widely spaced pulses can be transmitted. Since the muscles incorporate a low pass filter characteristic, the position of the eyes would be maintained better than would be suggested by the intermittent nature of the pulses.

The description of the signals used in the high frequency portion of the system are more difficult to describe since they are not repetitive in time. These are the signals, under control of the PGN/pulvinar couple, that are used to scan the imagery presented to the foveola. The scan pattern used by the eyes is unknown at this time. However, in its simplest form, it can be thought of as a two dimensional raster scan as used in conventional television. Under this assumption, the signals to the muscles of the high frequency portion of the servo system can be better described as individual pulses applied to one of each pair of muscles in order to cause an oscillation of the line of fixation back and forth about a mean position. To achieve a raster scan, the frequency of these two sets of pulses would be significantly different. The limited data available does not indicate that this is the condition observed in practice. It appears the PGN/pulvinar couple calls for a more complex, scene dependent scanning strategy.

15.3.5 Computational capabilities of the servo loops

The immense computational capabilities of the brain have not been defined to any level of detail in the literature. This section will address some of these capabilities related to the functional aspects of scene interpretation and symbolic interpretation (most commonly in the form of reading). Underwood has recently provided a comprehensive overview of what is known about the tasks of scene interpretation and reading. By relating the features of the servomechanisms of vision outlined above to what is known about the operation of the eyes in scene perception and reading, a general outline of the computational mechanisms used in vision can be obtained. Figure 15.3.1-11 provides a conceptual model of the computational paths in the servo loops of vision. This figure subdivides the perception task into a number of operating modes associated with computation (compare with Sections 7.3 and 7.4 where these modes are further subdivided and the dynamics of these circuits are discussed). These modes include two modes that operate to a large extent in parallel. The awareness mode is associated primarily with the extra-foveal photoreceptors of the retina. The analysis mode is associated primarily with the foveola. These two modes provide information to the cerebrum over distinctly different signal paths. Both paths converge in area 7. The awareness path maintains a spatial relationship to the scene in object space until after the LGN and passes information to area 7 via areas 17-18-19, etc. This process path is long and takes time. The analytical path is designed to be much shorter and operate on a much shorter time cycle. The data is vectorized in the PGN/pulvinar couple and sent directly to area 7 (and quite likely to areas of the cerebellum specializing in reflex responses). An alarm mode is defined that appears to draw its signal information primarily from the combination of Reyem’s Loops and the LGN. There is also a volition mode, by definition a response to the will of the higher cognitive centers of the mind. The figure makes certain tentative assignments of function to specific morphological features of the brain. These will be addressed specifically in later sections. Although complex, this figure is still far from complete. The next figure will expand on the considerable complexity of the analysis mode of the system.

There may be another mode that is frequently suggested in the literature. In response to an alarm, the system will attempt to change the line of fixation to agree with the point of interest. If this point of interest has moved substantially, another alarm may be issued that will cause another saccade. This syndrome prevents the visual system from entering the analytical mode and can be described as a tracking mode.

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Figure 15.3.1-11 Computational paths and engines associated with the servomechanisms of vision. See text.
Note specifically the double bordered boxes in this figure. These are the key elements in perception within the visual system. These elements are responsible for converting specific portions of the imagery of object space into vectorial information in cortical saliency space. The process employed by these elements are discussed in Sections 7.5 and 15.4. Both of the above figures begin to illustrate the various uses of memory in the visual system. There appears to be very short term scratch memory associated with the analysis function, short term memory in the routine operation of the feature extraction and feature extraction activities of the cerebrum and long term memory to provide historical references. In the case of reading, it is clear that the system relies upon long term (apparently permanent) memory to provide a vocabulary and set of syntactic rules (for each language known to the individual), on short term memory to assimilate the meaning of individual character groups analyzed during the “reading” of a long word, and on medium duration memory to assimilate the content of a paragraph, page or book.

15.3.5.1 Visual suppression as a mechanism during saccades

There is a large inventory of experiments showing some form of desensitization of the visual system related to the movements of the eyes. This applies particularly to the larger saccades. MacKay has provided a minireview with references300. Robinson & Petersen have provided a more recent study related primarily to blanking in the pulvinar301. Sylvester, Haynes & Rees have recently provided a paper summarizing what is known concerning blanking in the visual system and providing data from an MRI using the BOLD (Blood Oxygenation Level-Dependent) configuration302. They support the view that the operation of the blanking function occurs sufficiently early as to effect both LGN and V1 signals. This supports the view here that blanking occurs within the diencephalon under the control of the TRN and based on signal generation within the POS.

A recent discussion of this subject has generated additional research303,304,305,306,307.

This blanking function will be described as a responsibility of the thalamic reticular nucleus in Section 15.6.

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15.3.6 Features of specific morphological and functional elements of the POS

15.3.6.1 Analogy of the vestibular system to an inertial platform

As noted above, the vestibular system is tasked with providing orientation information to the thalamus and superior colliculus so that the animal can maintain its orientation within earth oriented inertial space. This function is not significantly different than the inertial reference systems developed by man.

Both the vestibular and man-made gyroscopic reference packages are of the strapped down variety. They are “bolted” to the frame of the overall system. In the modern man-made systems and the vestibular system, the reference package can be described as a group of orthogonal ring gyroscopes. In both cases, the ring gyroscopes are designed to provide an output signal proportional to a change in the rotation of the ring that is about an axis perpendicular to its plane. The man-made gyroscope does this by measuring the speed of light around the loop. The vestibular system does this by measuring the pressure developed by a fluid within the loop as the fluid tries to move within the loop due to inertial forces. In both cases, the output signal is characteristic of a first order servo loop. It is proportional to a change in position but not indicative of the absolute position of the sensor. To overcome this shortcoming, the overall vestibular system must obtain an absolute orientation signal from a separate source. This source is the orientation sensitive feature extraction engine of the visual cortex. Pansky, et. al. shows the signal from this source emerging from the Interior sagittal striatum of area 18 on page 325.

It is predicted that this signal from the interior sagittal striatum consists of two separate neural paths that carry difference type signals that are orthogonal to each other. The function of these combined signals would be similar to the polarization difference signals from the retina of many animals, to provide an absolute angular reference extracted from the available (primarily visual) input information. This (these) absolute angular reference signal would be equivalent to and serve the same purpose as the pendulum (or compass in different applications) associated with a man-made inertial reference package.

Taube & Bassett have described the operation of the neural circuits of the POS that rely upon the vestibular system in considerable detail. The mechanisms appear to mimic the typical servomechanism resolver in action.

15.3.6.2 Analogy of LGN to a boolean null detector

Reviewing the requirement of the Precision Optical System for an error signal to insure proper stereo-optic viewing and the information available about the role of the LGN in merging the images from the two eyes, it is logical to expect a command signal to be generated by the LGN for this purpose. It is proposed that the LGN uses conventional boolean algebra and comparator circuitry to provide this signal. If the signal manipulation layers of the LGN employ relatively small neurons to process the analog signals recovered by the stage 3 decoders, it is easy to make the output of these analog neurons binary in character. If the neurons are used in a differential mode, similar to that used by the bipolar neurons of the retina, the output signal will be a binary representation of the difference between the two input signals. By combining these binary output signals from groups of neurons, in a time coherent manner, a signal can be obtained that is bipolar in nature and exhibits a pulse width that is indicative of the error in registration between the two input images. This signal can be used to specify the error in stereoptic registration as required by the POS. At least two orthogonal signals need to be created to support the pitch and yaw servomechanisms of the POS. There may be a requirement for a roll signal as well.

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It should be noted that the signals from the foveola are not useful in this signal generation process, compared to the signals from more distant points in the retina that provide a greater lever arm in the calculations. Alternately, the image quality of the lens group becomes poor in the periphery of the retina. The area surrounding the foveola, the fovea and the parafovea may be ideal sources for information to be used in the extraction of stereoptic correction signals. This situation is consistent with the record that shows the signals from the foveola do not pass through the LGN.

Based on the above computational capabilities of the visual servo systems and the time delay introduced by Reyem’ loops, it appears that the LGN can provide three error signals of importance in vision. By computing a global difference between the time of arrival of the signals, across the retina, as a function of the vergence angle of the eyes, it can provide a stereoptics nulling signal. By providing a local difference in the arrival time of the signal from the two eyes relative to the global signal, it can provide cues as to the range to the specific object causing that local difference. By providing local differences in the spatial rate of change of illumination with respect to position of nearby elements of the scene, it can provide a cue to the informativeness of that region of the scene. By providing local differences in the temporal rate of change of illumination, it can provide alarm cues indicative of possible threats in object space.

15.3.6.2.1 Parallax, stereopsis and the thalamus

Hubel has written extensively on the concept of stereopsis\textsuperscript{310}, the process of merging the signals obtained by two separate sensing devices in order to remove parallax errors and to obtain cues as to the distance to different objects within a scene. His work has concentrated on the conceptual aspects of merging spatial information in the LGN’s of the visual system. He has not defined the mechanisms that support this process nor considered the temporal aspects associated with it.

The thalamus appears to support all of the calculations associated with the phenomena of parallax whether related to vision or the auditory system. The auditory system accomplishes the determination of the direction to an audible source based on the difference in the time of arrival of the audio energy at the two ears. Vision cannot employ time of arrival in this manner because of the much greater speed of light. The visual system can employ the same concept however, if the eyes introduce a time delay proportional to position of a feature in object space. This is done via the optic radiation associated with the axons of the ganglion cells of the retina. Upon reaching the LGN’s, the left and right LGN’s appear to operate independently initially, the signals are compared in correlation circuits without the aid of any additional time delay circuitry. The correlation circuits compare the arrival time of the signals about individual features in the object space.

Hubel has noted that stereopsis only occurs in the plane determined by the location of the two eyes and their lines of fixation. For features in object space displaced more than a few minutes of arc in pitch relative to this plane, the visual system considers the features to be separate. For two isolated discreet features in object space and the plane of fixation defined above with a separation of less than two degrees, the thalamus will perform signal manipulations aimed at merging the images of the two features, whether appropriate or not. In the presence of more features in object space, the thalamus will attempt to determine an average convergence correction signal that will attempt to correct the majority of the scene for parallax. Hubel has noted that two degrees is approximately 0.6 mm on the retina. The extent of the foveola is only about 0.35 mm in diameter. The extent of the fovea is about 1.85 mm in diameter. It appears that, the ability of the visual system to correct for parallax error and generate depth perception is associated with the region of the fovea outside the foveola, since those signals do not go to the LGN’s, and extending to about one-third to one-half the diameter of the fovea.

As noted above, stereopsis only occurs with respect to the yaw angle of vision. Therefore, the correction signals need not contain an orthogonal pair. It appears that the correlation circuits in the stereopsis engines of the thalamus generate two categories of output signals. A global average parallax correction signal is generated by each LGN and

delivered to the pointing engines of the Precision Optical System. These signals are used as differential signals to the two oculomotor nuclei associated with the yaw channels of the pointing systems. When the eyes have been turned differentially to null the contribution from these two signals, the eyes are properly converged on the features in object space closest to the line of fixation and most important to the visual system.

An additional signal, or tag, is generated applicable to each significant feature in the two degrees of object space surrounding the line of fixation. These signals are formed by subtracting the parallax signal associated with the individual object use from the global average parallax signal to produce a tag that can be associated with the complete vector describing that object.

15.3.6.3 Pathological Conditions related to servo loops of the eye

A large variety of observable pathological conditions can result from failures in the POS.

+ A failure of the connection between the 2nd lateral matrix and the PGN can result in a very unfortunate condition where the subject can see perfectly. However, he/she can not perceive and recognize new images, of both familiar and new objects, on the fovea.

+ A complete failure of the flick and tremor generator is a serious condition. The eye reverts to its fundamental change detector mode of operation. The subject is functionally blind although he/she reports seeing ghostly figures moving across its field of view under various conditions. These may be due either to movement within the image field itself, to change in the subjects line of fixation due to saccadic motion, or physical motion of the head or body that can also cause relative motion of the line of fixation relative to the scene.

+ Failure of the connections between the vestibular nucleus and the terminal nuclei of the AOS can result in a variety of clinical conditions related to nystagmus.

+ Failure of the connections between the PGN and area 19 of the posterior cortex will not destroy the perception of images but it will considerably reduce the richness and meaning of the sensations related to the image.

Specific problems related to failures in stereopsis are addressed in Section 18.8.2.

15.4 General mechanisms in visual perception

This major heading will discuss perception without focusing on the foveola and the specific activities of the POS related to the analysis of fine detail and reading. This section will also overlook the critical aspects of learning and recall as they relate to vision. Without memory, and the ability to learn, the animal is largely equivalent to a plant.

This section will begin to discuss the multiple steps of perception (cognition) that occur in both the “old brain” and the neocortex. Until recently, the common wisdom (subject to a dissenting minority) has been that cognitive functions related to perception only occurred within the neocortex311. It will be necessary to develop more distinct definitions for the terms cognition, perception interpretation etc.

15.4.1 Spatial and Temporal relationships relating to perception

Considerable new information has become available in the last few years on the location and characteristics of the mapping of the cortex and of the time relationships between different facets of perception. Zeki & Moutoussis have

shown that the brain does not correlate the information related to a given scene with respect to time in object space. It correlates the information it gathers at the time it is perceived in cortical space. They describe this process as a misbinding of the relevant features. This can introduce significant perturbations between what is imaged and what is perceived (a feature known to magicians for a very long time). In discussing the difference in time between the color aspects of an image and the motion aspects, time differences of 50-100 ms have been encountered with the perception of color always occurring first. They speculate on the utility of a precise clock within the visual system to allow information to be tagged at the retina and then reassembled at the perception or cognition level without any time distortion, i.e. correct binding, but their experiments do not support the presence of such a synchronizing capability. They conclude that the brain appears to ignore real time and synchronize with respect to its own time, a situation they described as ingenious and counter-intuitive. Based on this work, the binding of features based on their time of perception appears to be completely rational and avoids additional circuit complexity that is not required in normal vision.

They have also concluded that the earliest feature extraction with respect to color occurs in V4 whereas the cells of V5 are apparently indifferent to color.

Moutoussis & Zeki have also presented two significant papers. Much of their color oriented experiments do not account explicitly for the state of adaptation of their subjects. Neither do they recognize the temporal asymmetry associated with stage 3 processes according to this work. They do not present any signaling model as part of their expositions. In the second paper, they discuss the dismissal, in recent years, of the visual system as reproducing reasonably faithful topographical maps of the retina within the various cortical areas. The realization has become firmly established that perception involves a broad variety of feature manipulation and extraction sites that bear little relation to the topography of the retina. This has led to the realization that the different feature extraction engines might have tasks of different difficulty to perform and might require different time intervals to perform them. As a result, the overall perceptual process is neither synchronous, nor even performed with fixed delays between signal paths. In their paper, they espouse the idea of Land in his Retinex Theory that the perception of color requires the knowledge of the color within a contour as well as the color found in the surrounding scene. This is a different proposition than baselined in this work that the signal manipulation stage can assign a chromatic characteristic to the area immediately adjacent to a contour (subject to the state of adaptation of the various photoreceptor channels involved and the asymmetries of the signal projection channels). The difference is a subtle one in practice and may require significant improvements in instrumentation before it can be resolved. Their attempt to combine color and form through the premise that every border has a form (apparently more complex than a mere edge) appears awkward.

Most recently, Seki & Bartels have summarized much of the findings of the group over the last few decades. One of their major conclusion is that the various feature extraction engines are also the seats of perception and they should be described as processing-perceptual systems. If this be the case, they will be called feature extraction & perception engines in this work in order to maintain continuity. They suggest that it is this binding of the perception achieved by each of these sites that leads to our integrated image of the visual world. The conclusion is drawn that the visual brain is modular in its organization and there is no hierarchal center of overall perception. They also conclude that areas V1 and V5 are focused on feature extraction related to motion and that V2 and V4 are focused on feature extraction related to color. Additional areas surrounding V5 have been found to be specialized for extraction of motion related features such as rotatory motion, biological motion and optical flow, in both monkey and man.

They also correlate much of the data available from lesions and accidental damage to the cortex with the above.

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conclusions relative to modularity. As an example, they say “It has now been shown conclusively that patients with a damaged area V1 and an intact area V5 can still discriminate and experience consciously fast motion presented to their blind hemifields.” Most of these examples emphasize the discrete modularity of the cortical portion of the visual system, as opposed to the parallel nature of most of the subcortical processes in vision.

A key point is that none of these areas of the cerebral cortex have been related to the extraction of fine detail and the ability to read. These functions are the domain of the PGN and pulvinar of the midbrain.

15.4.1.1 The general parameters of the two-dimensional correlator of the PGN

While the details related to the correlation function of the PGN remain sketchy, some parameters are beginning to appear. The paper by Levi can be mined for much information if the basic premise of the eye as a change detector is accepted

15.4.1.1.1 The spatial parameters

The correlator serves an area that is roughly circular when referred to the retina and encompasses a one-to-one relationship with the photoreceptors of the foveola. This would suggest an overall correlator size of 23,000 elements with a diameter of about 175 pixels. This would correspond to the central 1.18 degrees of the field of view in object space. When operating at maximum performance, it is able to extract interps at a finesse on the order of 5 to 10 times better than the finesse associated with the dimensions of the photoreceptor matrix. This performance is based on the change detection capability of the visual system combined with the tremor mechanism and is not related in any way to the opertion of the eye as a pixel limited imager. The values processed in the correlator are related most directly to the edges associated with the fine detail in the scene and not their absolute position. This is based on a vernier acuity of about six arc-seconds (0.1 arc-minutes) compared to a Snellen acuity of 0.8 arc-minutes.

15.4.1.1.2 The temporal parameters

The correlator appears to operate on an internal time cycle determined by the frequency of the tremor generator. It is on the order of 10 msec. The output time cycle of the correlator appears to be on the order of 50 msec. This would suggest the correlator includes an auxiliary correlator that defines an interp based on several correlations. These individual correlations may be based on individual scanning directions as specified by the tremor generator. The interplay between the correlator and the tremor generator may be very close within the nominal 50 msec cycle.

15.4.2 Perception of Shape/Form & motion

The analyses of the processes involved in the perception of shapes is at the leading edge of the state of the art in perception by the visual system. The understanding of the more advanced perception of glyphs (abstract shapes) and letter groups are even less well understood since these capabilities are, to a large extent, limited to the human species. As one proceeds down the phylogenic scale, the capabilities of animals to recognize specific shapes is remarkable but these are not abstract shapes. They are generally shapes related directly to its search for food, and to a lesser extent its search for safety from predators.

The perception of primitive shapes and the subsequent interpretation and recognition of these shapes as glyphs and letter groups involves a different domain of signal manipulation than in the previous discussions. The mechanical aspects of the scanning of images employing tremor has been introduced in Section 7.5. Its role in reading will be

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The perception of shape and form is accomplished using a variety of techniques in vision (particularly in human vision). Possibly the crudest techniques involve the tracking of gross shapes by the oculomotor system. The most sophisticated is the cross correlation of two dimensional brightness information within the PGN of the Precision Optical System. These techniques will be discussed below.

15.4.2.1 Perception of Shape/Form by the PGN

A mechanism that may be limited to humans (or may include a few of the higher apes of superfamily, *Hominoidea*), is the two dimensional cross correlation of image information within the pretectum of the Precision Optical System. It is this capability, aided by the lookup tables stored in the cerebellum (and possibly elsewhere), that separates humans from all other animals and allows it to read.

The PGN operates as a two dimensional cross correlator on the raw (not spatially or spectrally encoded) information provided to it over the “straight through” signal paths. These paths extend from the photoreceptors of the foveola to the PGN via the second chiasm of the optic nerve. The information from both eyes is combined to achieve higher performance. This is possible because the oculomotor servo loops of the Precision Optical System have already performed stereopsis based on both internal signals and those obtained from the LGN.

It appears that the PGN treats the signals from all of the photoreceptors of the foveola equally without regard for their individual spectral sensitivity. This approach leads to the highest spatial resolving power at the possible expense of some sensitivity.

The nominal extent of this cross correlator is a circle of approximately 175 elements in diameter. The responsibility of this correlator is to extract the spatial characteristics of the image presented to it in a highly abstract form. It then either (1) compares the extracted parameters with the information stored in the cerebellum and reports the identification of the identified pattern to the cerebral cortex or (2) provides the extracted parameters to the cerebral cortex and determines in a collegial process the value of the data set. The result of this cognitive process is then stored for future reference.

The properties of the two dimensional cross correlator of the PGN are essentially unknown. Man has only created a few similar correlators. These have usually been so task specific that they do not relate easily to the task faced by the PGN. Examples include the analog correlators used in side looking radar and similar sonar applications. They also include the class of computers known as parallel processors. Again, these have usually been used in task specific applications and usually in a multi-bit digital word environment. A technique that is similar to the problem faced by the PGN has been the use of two-dimensional Fourier Techniques in the optical analysis of images illuminated by coherent light (holography). This technique has allowed machines to scan text material and identify individual syllables, words and occasionally simple phrases. Poorer results have been obtained using incoherent light. These techniques are probably based on the same class of mathematical techniques employed by the PGN.

For purposes of this Chapter, an individual output of the PGN/pulvinar couple will be defined as a signal in vector form known as an “interp”. An interp arises from the cross correlation of the information presented to the PGN by the foveola during a single gaze interval. The interps are transmitted individually to area 7 of the cerebral cortex where they are accumulated in a short term annex of the memory holding the saliency map. The interps are accumulated sequentially until they are perceived to contain a complete thought or message. This group of interps is then assembled into a single vector signal that is stored in the saliency map. The higher cognitive centers access this map, which also includes other sensory inputs, in order to obtain a complete picture of the environment.

The role of the pulvinar is to act as a image matching device. It compares the image currently applied to the PGN to previously stored images (based on experience and learning) and delivers an output interp or percept to the saliency map. The importance of experience in fine vision has recently been documented by a subject, Mike May, who
recovered his vision in late middle age after being blind since three years old due to a chemical accident\(^\text{317}\). When a successful cornea replacement was achieved, May reported an ability to perceive color and motion in considerable fidelity but he had great difficulty in reading, and perceiving detail in scenes. This difficulty stresses the necessity of learning and experience in the operation of the PGN/pulvinar. Because of his age, May will probably have difficulty learning to see fine detail.

15.4.2.2 Perception of Shape/Form, using external feedback RESERVED

- Perception of stationary scenes
- Geometrical fidelity of scenes
- The Blind Spot
  
  [[ see Ditchburn pg. 242 ]]

see auxiliary optic system in Rodieck ‘98 pg 269, 271 & 321-325 rename this the precision optical system or something similar. It analyzes, not stabilizes. See also pg 296 reference copy.

Skavenski ‘79 used magnetic coil method that was limited to a fraction of a degree accuracy.

[See also section 7.5 on the perception and dynamics of reading etc.

15.4.2.3 Perception of motion RESERVED

Oyster 68, Oyster 72 and Rademaker & Ter Braak 48
different in primates and lower chordates

Oyster did not appreciate importance of oblique muscles in correcting axes.

15.4.3 Perception of luminance

[xxx This section overlaps Sections 16.3.2, 16.3.4 & 17.2. Except for portions directly related to perceptual by the CNS, it will probably be consolidated with those sections at a later date.]

The figures in this section are presented using linear scales for the convenience of those readers who prefer that format. However, some details are lost using this format. Equivalent figures plotted using logarithmic amplitude scales will be found in Section 17.2.

As discussed earlier, the intrinsic visual process in animals is tetrachromatic. There are many animals in diverse phyla that are demonstrably tetrachromatic, including aphakic humans. This requires the discussion of the perception of luminance to be subdivided depending on the photoreceptors involved. As an example, Neumeyer\(^\text{318}\) presented a spectral response caricature for tetrachromats that is quite interesting. It is a composite from data of a number of researchers. This type of data is difficult to obtain because of the low signal to noise ratio in the response data. Douglas, et. al. demonstrate this situation\(^\text{319}\). When the signal to noise ratio is very low, it is difficult to describe the character of the individual spectrums. Whereas, Neumeyer & Arnold show the Y (M-) channel as the


\(^{318}\)Neumeyer, C. (1988) appears as fig. 5 in Neumeyer and Arnold

widest and X (S-) channel the narrowest, Partridge and De Grip say the L-channel is wider than the M-channel. Both base their claims on the Gaussian assumption as to the shape of the spectrums and neither recognized the square law nature of the L-channel which further complicates such comparisons. Figure 15.4.3-1 compares the caricature of Neumeyer & Arnold with the calculated spectrums proposed in this work. The proposed spectrums are based on Fermi-Dirac statistics. These statistics introduce the characteristic flat tops of real chromophores, and are based on a constant, Q=4.8, for all chromophoric channels. The short wavelength cutoff of the ultraviolet data is limited by the transmission of the fish lens (dashed line). It is possible that the family of actual chromophores do not exhibit a constant Q. Further investigation is needed in this area. The “tails” leading off to the left in the Neumeyer and Arnold waveforms are due to the xxx absorption band of the retinoid molecule. Similar tails can be introduced into the theoretical spectrums if desired using the data of Chapter 5.

In (b) of this figure, the tetrachromatic spectrum is further subdivided to show the spectrums of two subclasses of visual systems. The short wave trichromats, primarily found among Arthropoda, have chromophores with center wavelengths at 342, 437 and 532 nm. The long wavelength trichromats, primarily found among the large members of Chordata (and including humans) exhibit spectra with center wavelengths at 437, 532 and 625 nm.

A significant number of electrophysiology studies have now confirmed the facts related to these center frequencies at the output of the signal manipulation stage although the experimenters have frequently used various templates to define the shape of the individual spectrums. The use of templates, which have usually been Gaussian or parabolic in shape (or of the Dartnall type), has generally misrepresented the actual spectral responses.

Zeki has provided the only data available on the spectral response of the individual chromatic channels of the visual system determined at a point within the cortex of the rhesus monkey. He has presented a group of about nine individual spectrums. Three of these spectrums, the two at the extremes of the visual spectrum and the one in the center correspond precisely, well within his error tolerances, with the peak wavelengths predicted by this work. For the extreme spectrums, he gives peak values of 438 ± 14 nm and 631 ± 14 nm versus the predicted values of 437 ± 2 nm and 625 ± 2 nm. His peak wavelength for the M-channel, read from a graph, is 514 nm versus the predicted value of 532 ± 2 nm. He did not present data points in his graph, only curves obtained by overlaying a parabolic curve to his data “in the conventional way.”

His instrumentation was quite limited and each spectral characteristic only extends over an amplitude of less than 30:1. For reasons not explained, his spectrums exhibited a wide range in half amplitude widths. The widths were typically quite narrow, with half-amplitudes for the above three absorption spectrums each varying between 10 and 50 nm compared to the width of about 95 nm for each spectrum as predicted in this work and shown to be

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\[^{320}\text{Partridge, De Grip, XXXX}\]

compatible with the human luminous efficiency function.

He did not present any model to justify the use of a parabolic template nor did he provide the eccentricity of the parabola. Lacking a model, it is difficult to discuss whether a Fermi-Dirac template would have been more appropriate.

A major feature of the Zeki paper was the inclusion of a series of transparent filter strips with peak transmission wavelengths matched to his observed wavelengths as closely as economically feasible. These strips have peak wavelengths at 429, 527 and 625 nm (although the L-channel simulation is actually a long wavelength pass filter). Although the peak amplitudes were not adjusted to represent the absorption coefficients of the human eye, the filters can be very helpful in visualizing the absorption spectrums of the human chromophores. It should also be noted that these filters are transmission as opposed to absorption filters. The skirts of the transmission spectrums are of intrinsically different shape than found in the absorption characteristics of the chromophores of vision. The width of the spectrums should not be taken as representative of the visual process. These filters are bound in the front of the journal and are available to anyone by retrieving the paper from his local library.

For the remainder of this Chapter, where it is important to relate many of the signals of vision to their actual perception, the scope of the discussion will be restricted to that of the human observer.

For the convenience of the reader, the remainder of this section will ignore the ultraviolet sensitivity of the human eye and the consequences of that sensitivity in the region between 400 and 437 nm. Human sensitivity in this area is of greater significance when discussing the chromatic performance of the visual system. Even ignoring the intrinsic ultraviolet performance, some of the theoretical curves will still show sensitivity in better agreement with the photopic visibility functions of Judd and of Weaver than with the CIE (1924) Photopic Standard.

Because adaptation is such a major factor in human vision, it has been difficult to define the sensation of luminance precisely in mathematical terms. Instead, since early on it has been generally recognized that there is a region of “photopic” vision, or vision under “high” levels of illumination and a region of “scotopic” vision corresponding to “low” levels of illumination. Later, it was recognized that there was a continuum between these two levels, which came to be called the “mesopic” region. In addition, it was found by Bezold-Brucke that at higher illumination levels within the “photopic” region, the perception of color continued to change as a function of illumination. This effect will be found to occur naturally within the hypertopic region as discussed below. The conclusion to be drawn from the above is that the perception of color is a specific function of the illumination level with four separate illumination regions clearly identifiable. These regions of human vision can be clearly defined as:

+ a scotopic region of very low illumination wherein the L-channel of vision is inoperative

+ a mesopic region in which the participation of the L-channel of vision is becoming more important, and where the Purkinje phenomenon is frequently encountered.

+ a photopic region in which the three channels of vision are operating at their normal (relative) levels

+ a hypertopic region in which the M-channel is depressed relative to its normal level with respect to the S- and L-channels, the region associated with the Bezold-Brucke phenomenon.
The perception of light differs dramatically between the photopic region and the other regions described above. Within the photopic region, the adaptation processes associated with each spectral channel are fully operative. The phenomena of color and brightness constancy result from the adaptation mechanism. Because of these phenomena, the CNS receives information about the external stimuli that is highly standardized. Outside of the photopic region, color and brightness constancy are not maintained. At light levels below the photopic region, the signals received by the CNS are more nearly a direct analog of the stimulus received by the retina.

The photopic region will not be treated in detail in the remainder of this section as it is explored in detail in Sections 16.3 & 17.2.

15.4.3.1 Fundamental sensation of luminance within the CNS

While it is easy to document the amplitude of the luminance signal as a function of wavelength external to the brain, it is more difficult within the brain. The information as to how the stellate cells decode the R–channel signals is very conceptual at this time.

There are two distinct possibilities which may differ only in the time constant of the stellate cell output circuit. The stellate cells of the brain may act as “linear demodulators” and recover an electrotonic signal representing the amplitude signal transmitted over stage 3. Alternately, the stellate cells may act as an “exponential demodulator” and recover the amplitude of the signals based on the supposition that they were logarithmically encoded only for transmission. The difference in amplitude between the R–channel, representing the sum of logarithmic terms, and a potential antilog of that channel, \( X(\lambda, F) \) is shown in Figure 15.4.3-2. The symbol \( X(\lambda,F) \) is used here to describe the brightness signal recovered in the brain and corresponds to the \( Q \) (sometimes \( C \)) frequently used in the basic equations of colorimetry to define the external stimulus. \( X(\lambda,F) \) is calculated using the logarithmic base ten for convenience. A stimulus situation exhibiting the Bezold-Brucke Effect (see Section 15.4.3.2.1) was chosen to emphasize the potential differences.

When plotted normalized at a wavelength of 532 nm, several differences are notable. The antilog form tends to accentuate amplitude deviations relative to the normalizing value. The shoulders at 437 and 625 nm are also representative of the amplitudes of the input stimuli at these wavelengths compared to 532 nm, in \( X(\lambda,F) \). This is only approximately true in the case of \( R(\lambda,F) \).
While the difference in the two signals is not great, only one of them is likely to be used in practice. It is a challenge to the empirical community to determine which one appropriately describes the actual perceived luminance in humans (and probably other animals).

No detailed equation for the perceived luminance sensitivity (brightness sensitivity) of the human eye could be found in the literature, at a single luminance level or as a function of luminance. There is considerable data on this subject but no equation. There are a number of reasons for this;

+ no comprehensive theory based model has been available to define the luminance function.
+ most researchers have been willing to rely upon various empirical templates to describe each individual chromatic channel.
+ experiment design and calibration is difficult when unrecognized variables are present.

This work has presented a very detailed model of the visual process and the equations related to that model. This has led to new findings with regard to the perceptual process.

15.4.3.1.1 Potential introduction of $T_R(\lambda,F) \& T_C(\lambda,F)$

Up to this point, the threshold luminance function of vision has been defined as $T(\lambda,F)$ based only on the signal in the luminance channel, $R$, and a conceptually constant threshold in the signal to threshold calculation. The above discussion suggests that this definition needs to be modified to allow for two different cases. In the first, the
threshold luminance function would become, \( T_R(\lambda,F) \), based on a linear recovery of the luminance signal by the CNS. In the second, the function would become, \( T_C(\lambda,F) \), based on an anti-logarithmic recovery of the luminance signal by the CNS. Both formulations would still assume a fixed threshold but would reflect the difference in decoding technique. Which provides a better description of the actual perception of the system is yet to be determined.

Until further data becomes available, this work will continue to consider \( T(\lambda,F) = T_R(\lambda,F) \). This is based on the assumption that the stellate cells act as linear decoders.

### 15.4.3.1.2 Background

There have been many attempts to algebraically define the overall human luminance threshold function by algebraically summing the three chromophoric absorption spectra of human vision, and the converse, attempts to determine the L-channel absorption spectrum by subtracting the S-channel and M-channel responses from the standardized photopic response curve. These attempts have not been successful. Similar graphical attempts have also been unsatisfactory. The problem is complicated by the variable gain associated with each chromophoric channel of the system.

Figure 15.4.3-3 is a good example of the experimental difficulties associated with the determination of the spectral response of the human eye. Hurvich and Jameson\(^{322}\) show ten consecutive spectral sweeps (collected within a period of 1 to 1.5 hours) of the response by Observer H when “white adapted”. They represent that the conditions did not change during the recording session and appear to have taken considerable care. Thus the considerable variation between individual waveforms could be assigned to random processes in the experiment. However, this is unlikely; note the systematic development and movement of a shoulder in the region of 425 to 450 nm. in spectra 4 through 10. Similarly, in the 675 nm. region of spectra 7 through 10. And finally note the flattening of the central broad peak as the spectra number increases. According to the model used here, these trends are statistically significant. Looking carefully at the region between 425 and 450 nm in traces 7 through 10, it is seen that there is a local maximum in each trace (small but measurable in trace 9). This local maximum is closer to the true maximum value in each trace, for traces 7 through 10. This is a clear trend indicating that the test conditions were changing in a deterministic way. A similar change can be recognized in the region near 650 nm. The inevitable conclusion is that the luminous threshold function of Observer H changed during the observation period in a systematic manner. The M-channel sensitivity was reduced by 20% relative to the S-channel and the L-channel sensitivity was reduced by 20% relative to the M-channel. Hurvich & Jameson proceeded to average the ten waveforms in order to obtain a composite spectral response for Observer H under white adapted conditions. This resulted in the loss of the detail related to the systematic variations discussed above. Even with this loss, they did report “the sensitivity functions show a marked shoulder in the short wave region starting at about 450 nm.”, “show inflections at 490 nm”, and “have inflections in the long-wave spectral region at about 600-620 nm,” they did not investigate these features further. These are the very features that are demonstrated by the theoretical luminous threshold function of this work (See Section 15.4.3.1.3 below).

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If one accepts the premise of this work;

+ that the luminance information is transmitted to the CNS by a distinct signaling channel, the R–channel,

+ that the information in this channel is transmitted as the instantaneous sum of the potentials at the pedicles of the individual spectrally selective photoreceptor cells, and

+ The potentials of the individual pedicles are logarithmically related to the current generated by the stimulus,

the Hurvich & Jameson figure can be interpreted more fully.

As will be seen below, these additional features in the overall spectral response provide a sensitive test for determining the relative amplitudes of the signals in the three channels. These values contribute to determining the relative amplification factors (gains) in the three channels, and the relative density of the spectral photoreceptor types in the retina.

These features can also be used to determine the half amplitude wavelengths of the individual chromophoric channels.

The laboratory problem is complicated by the relatively flat top on the individual absorption spectra due to their foundation in Fermi-Dirac statistics. Most investigators in the past have assumed that the spectra were based on Gaussian Statistics and have attempted to fit their data to a Gaussian Function--or to one of the nomographs published by Dartnall. Another problem is the common practice of averaging the data from multiple experiments in a manner that leads to a more Gaussian waveshape (calling on the Central Limit Theorem) than called for. The accuracy sought here is not compatible with these curve fitting procedures.

It should be stressed once again that the visual system responds to the number of photons (which vary in energy with wavelength) and not to the average energy in a band of the visual spectrum. Therefore, for the most accurate results, the investigator should base his work on an equal photon flux per unit wavelength illumination source (preferably of
7,053 Kelvin) and not on an equal energy per unit wavelength source. A 7053 Kelvin source is near optimum over the spectral range of 400 nm to 700 nm. (See Chapter 2 or 5 or 16.xxx). Corrections can be made for lower temperature sources. However, for temperatures below 4000 Kelvin, the magnitude of the corrections becomes a consideration (and complication).

15.4.3.1.3 Design considerations

The voltage form of the overall luminance signal, as it appears in the R–channel, can be given by the following generic equation:

\[ a_t(\lambda) = \log(k_s \cdot g_s(\lambda)) + \log(k_m \cdot g_m(\lambda)) + \log(k_1 a_1(\lambda)) \]

Generic form, Eq. 15.4.3-1

where the individual spectral responses, \( a_t(\lambda) \) are those developed in Section 16.3.2 and 16.3.4. They are the product of the illumination source, the reflectance of the scene and the absorption characteristic of the particular spectral channel. The term \( a_1(\lambda) = R(\lambda) \). The constants, \( k_x \), are arbitrary at this point. However, their values are not the same as when operating in the photopic region. Since the adaptation amplifiers are operating at a fixed, and maximum, gain throughout the lower portion of the mesopic and all of the scotopic region, the relative values of these constants reflect the intensity of the source illuminance and scene reflectance directly. The only constraint on their value is that each logarithmic expression is either positive or zero (which is compatible with the monophasic nature of each chromophoric signal at the output of the photoreceptors). They still incorporate any factor due to the transfer networks between the photoreceptor cells and the bipolar cells of the retina.

Since the ganglion cells can generate pulses over only a limited range of pulse intervals, it is optimum to use the full range available for both the luminance and chrominance channels. The range of pulse intervals generated to the range of input voltages can be matched by adjusting the transfer network between the ganglion cells and their stage 2 driving circuits.

There is a choice to be made at the stellate cells of stage 3 that are located in the CNS. Should these cells be designed to recover the voltage signal used to encode the R–channel at the ganglion cells or should they be designed to recover a current analogous to that produced in an individual photoreceptor cell? In either case, the recovered signal will reflect to mechanism of logarithmic summation used in stage 2. A similar choice must be made in the chrominance channel stellate cells. Should the cells recover a voltage proportional to the pulse interval in the chrominance channels, which reflects the stage 2 voltage driving the ganglion cells or should they be designed to recover the antilog of the voltage driving the ganglion cells?

While it is not overly difficult to recover the antilog of the voltage encoded by the ganglion cells, it is easier to recover a voltage linearly proportional to the input pulse train (see Section 14.3.5). If the recovered signal is always proportional to the pulse interval, only copies of a single generic sensing circuit are required in the brain to process all of the signals received over the optic nerve. This includes both the monophasic luminance signals and the biphasic chrominance signals. No adjustments are even required for calibration (in the case of the chrominance channels, calibration errors may be perceived as a degree of color blindness). This is of great practical advantage. The associated ganglion cells would be required to have individually optimized input impedances, most likely based on long term average signal level. The associated decoding circuit could be as simple as a diode-capacitor circuit acting as a pulse integrator (basically an activa with a capacitor bridging the impedance in the poda lead).

If the recovered signal is always proportional to the original signal current, then the sensing circuits in the brain

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must exhibit different thresholding or bias values in order to recover the signal information from different chromophoric channels. This could be done in a number of ways, all of which involve additional learning abilities or differentiation during genesis in the animal.

15.4.3.1.3 Nominal condition

The many constants used to evaluate the following equations are the nominal values shown in Appendix L, The Standard Eye. All of the responses illustrated in this chapter were prepared using MATHCAD 6.0 and a family of programs titled c_human_spec_b.mcd. Calculations were performed at five nanometer intervals unless indicated otherwise. The amplitude of the peaks found near 490 nm and 580 nm are very sensitive to the precise difference between the half-amplitude values of the two spectral responses contributing to these peaks (and their position relative to the sampling interval). Since the precise values of these parameters are only known to about ±2.0 nm, the displayed responses can only be taken as illustrative at this time. It is likely that the precise values of these half-amplitude values vary with the effective length of the outer segments of the photoreceptors. This effective length may vary with location within the retina. In practice, the perceived height of the peaks may be an average over the field of the stimulus.

Based on the discussion of the previous section, the overall spectral response for a dark adapted human is shown in Figure 15.4.3-4 for the constants

\[ k_s = 20, \quad k_m = 1000, \quad and \quad k_l = 20 \]

using the routine c_human_spec_b.mcd in mathcad

It is necessary to show the response in two forms because the precision of the analytical response has seldom been achieved in the laboratory. This response is for a single triad of photoreceptors where each photoreceptor is of nominal physical dimensions (or a small group containing all three spectral types of photoreceptors). There is insufficient data on the minimum area that must be illuminated for the precise and repeatable perception of a specific chromatic response. However, the NTSC experiments of the 1950's showed that it was generally more than the diameter of one triad of photoreceptors. The minimum is likely to be on the order of a few minutes, to a few tens of minutes, of angle in object space (and vary with location in the retina). There is known to be a discontinuity in this parameter associated with the edge of the foveola.

The solid blue line in the figure shows the analytical function smoothed to represent data obtained using a 38 nm wide Gaussian filter. The peak of this curve remains very near 532 nm. The dash-dot lines are presented to show the effect of ignoring the S–channel (due to an inadequate light source or other cause). The dash-dot red line shows the upper skirt of such an analytical response is moved to longer wavelengths. The dash-dot blue line shows the smoothed version of this curve. The peak has move to about 550 nm under this condition. Note the significance of the dash-dot blue line to the left of 0.45 nm due to the width of the smoothing function. If the basic luminous response was re-normalized on an equal energy basis and then smoothed, the peak would move even further toward

\[ \text{Figure 15.4.3-4} \quad \text{The theoretical and smoothed spectral response of a dark adapted individual (linear scales). Solid red line is full response, } k_s = 20, \ k_m = 1000, \ k_l = 20, \text{ calculated at 5 nm intervals. Solid blue line is full response smoothed to 38 nm. The dash-dot pair shows the effect of ignoring the S–channel. Dashed line is CIE 1961 2' Photopic luminous efficiency function.} \]
long wavelengths and be in even closer agreement with the CIE defined peak at 555 nm. However, the difference is trivial considering the flatness of the peak and the limited accuracy of the CIE value.

There is another parameter determining the appropriate total smoothing factor. Because the illumination used in the laboratory has traditionally been larger than the foveola in physical diameter, has not exhibited a uniform photon flux per unit wavelength, has been pulsed at a generally unspecified pulse duration and repetition rate, and been filtered by a finite spectral bandwidth filter, additional calculations are needed to calculate the theoretical performance under the actual laboratory conditions. The response obtained in both electrophysiological and behavioral tests have always exhibited a smoothed characteristic. One can obtain some very interesting results by adjusting the smoothing approach and smoothing factor. If smoothing equivalent to a 10-20 nm. filter is used, a photopic luminance function is obtained not unlike that obtained by individual experimenters using the equipment available beginning in the 1940's. If smoothing equivalent to a 30-40 nm. filter is used, and the 400-450 nm region is ignored, a photopic luminance function can be obtained which is very similar to the C.I.E. Photopic Luminous Efficiency Function of 1924 (still in use today). These smoothed responses do not exhibit many of the intrinsic features of the original analytic function. However, they do accurately reflect the averaging performed on the raw experimental work of many in order to obtain the above C.I.E. function. The intrinsic features noted by various investigators have been treated as specific phenomena of unknown origin. Some of them will be discussed below.

The effect of smoothing is highly dependent on the kernal used in the mathematical operation. Any smoothing operation tends to distort the performance near the initial and final values of the data set. Many smoothing functions represent sharp transitions in the raw data differently. Section 17.2.2.6.6 discusses these variations in the kernal more completely.

### 15.4.3.2 The perception of luminance under general (unusual) conditions

Before focusing on the perceived luminance threshold function of human vision under what have become standard (but poorly defined) conditions in the literature, it is useful to review the perceived luminance under more varied conditions. This review will stress the importance of thinking of the visual system as consisting of three largely independent spectral signaling channels (except for some common aspects related to their metabolic energy supplies). It is only through understanding this independence that the characteristics of the luminance and chrominance characteristics of the overall visual system can be understood.

Note carefully that the peak response of the analytic functions in this section need not be collocated with the peak of any of the underlying individual spectral responses. Note also that the function has a number of inflection points and local maxima that are not reflected in the smoothed C. I. E. Function, although the inflection in the short wavelength region is recognized by the modification to the C.I.E. Function proposed by Judd, the chairman of the original standard working group. These inflection points and additional maxima are a result of the logarithmic processing in the visual system and cannot be accounted for under the general assumption of additivity and linearity so frequently found in the literature. The unique peak at 580 nm, and associated with the Purkinje Phenomenon is the one Wald mistook for the peak associated with the long wavelength spectral channel (see Section 15.4.3.2.2). It has been erroneously associated with the long wavelength spectral channel in humans ever since. Fortunately, this error has not been propagated into the non primate literature. The spectral peak in the long wavelength spectral channel of humans (and all other primates) occurs at 625 nm, as in all other species and phyla. Recall the earlier reference to Zeki in Section 15.4.3.

#### 15.4.3.2.1 Suppression of the M–channel, the Bezold-Brucke Effect

The Bezold-Brucke Effect has not been rigorously defined in the literature. Although the color names used and the nature of the change in illuminance are not adequately and scientifically defined, the phenomenon is usually described in the literature as; “when illuminance is increased, all chromatic colors except a certain invariable blue,
yellow, green and red appear increasingly like blue or yellow and decreasingly like green or red.” In this
description, the shift in perceived wavelength is all in one direction. With the availability of an overall signaling
model of the visual process in mathematical terms, the Bezold-Brucke phenomenon can be described in greater
detail. See Table 2.1.1 for the color names used in this paper and corresponding to the C.I.E. sanctioned names.
The model suggests the above description is quite inadequate. It is not the illuminance but the ratio between the
signals within the luminance, R–, channel that are important. Under conditions where the effectiveness of the M-
channel is reduced, the luminance response of the eye is perceived to exhibit an enhanced sensitivity to blue-green
(485 nm) and orange (580 nm). Simultaneously, the perceived chrominance response functions exhibit a shift away
from 532 nm in the mid portions of the P– and Q–channel ranges. The model also suggests the Effect only occurs
within the mesopic and hyperopic regions. It does not occur in the photopic region where “color constancy” is
maintained.

If the amplitude of the M-channel signal is suppressed, the relative importance of the S- and L- channels is
increased. Two separate phenomenon are observed, one related to the luminance channel and one related to the
chrominance channels. The first result is an increase in perceived spectral sensitivity in two regions of the spectra
that are not associated with actual chromophores. The Effect peaks near 485 nm. and 580 nm Figure 15.4.3-5
highlights this phenomenon. These are the wavelengths associated with the Bezold-Brucke phenomena. The
phenomenon is caused by the relatively high amplitude of the crossover points of the three chromophoric signal
channels relative to the peak of the M-channel.

The second phenomenon is a shift in perceived hue of
the scene. In the case of suppression of the M–channel
signal, the shift reflects the reduction in the peak height
of the M–channel component in the chrominance
discrimination functions of the chrominance channels
(see Section 17.3.2). The result is a shift in the null
value of the generated function, as a function of
wavelength, toward the peak wavelength of the
M–channel. This causes the recovered chrominance
signals in the CNS to represent a wavelength shifted
away from the expected M–channel peak.

The net effect of the luminance and chrominance
portions of the Bezold-Brucke Effect is complex. It
depends on the protocol used to measure the effect.
Does the protocol measure the combined effect or does
it separate and measure only one of the portions of the
Effect. It appears the net Effect is due primarily to
signal processing in the luminance processing channel
and due only secondarily to changes in the
chrominance channels. Walraven has described similar peaks as occurring at 476 nm and 570 nm. (see Section
17.2.3.5).

The Bezold-Brucke phenomenon is primarily a perceptual one occurring in stage 4 as a result of the signal
processing of stages 1 & 2. It is frequently manifest under transient conditions, particularly following differential
chromatic adaptation. It is difficult to directly relate electrophysiological tests limited to the retina to this
phenomenon.

15.4.3.2.2 Emphasis on the L–channel, the Purkinje Effect

The model has shown that the luminous threshold function of the human eye varies continuously with illumination
while operating in the mesopic region. The change is large in the long wavelength region due to the square law characteristic of the L-channel, and by a smaller amount in the short wavelength region upon saturation of the M-channel at high illumination levels. The Purkinje Effect is a close relative of the Bezold-Brucke Effect but it only involves the portion of the perceived spectrum between 532 and 625 nm. It is most often observed under transient conditions associated with sunset and a clear atmosphere.

Figure 15.4.3-6 illustrates the Purkinje Phenomenon based on the same equation used to define the Bezold-Brucke Effect. The Purkinje Effect is normally limited to the mesopic region where color constancy is not maintained. The Effect exhibits both a luminance and a chrominance component just like the Bezold-Brucke Effect. As the amplitude of the L-channel contribution approaches the amplitude of the M-channel contribution in the R-channel, an artifact appears with a peak near 580 nm. Simultaneously, the null point in the signal generated in the Q-channel moves to longer wavelengths. As describe above, the wavelengths of scene elements perceived by the CNS move in the opposite direction. The perception is that objects have become “greener” by tens of nanometers. However, this shift is not generally apparent because of the high level of “red” light in the overall scene.

A more specific restatement of these effects could be as follows:

**Purkinje phenomenon**—Within the mesopic region of vision, the perceived (and typically transient) increase in the brightness of objects or lights in the spectral range from 550 nm to 610 nm is significant. This perception is accompanied by a shift in the perceived color of an object to shorter wavelengths. However, this perception is usually un-noticed due to the dominance of red light in the overall illuminance.

**Purkinje shift**—The abrupt jump in the peak spectral sensitivity of the subject from 532 nm to 580 nm (and eventually back to 532 nm) as the light level transits the upper portion of the mesopic region.

The Purkinje Phenomenon is most often observed under the transient conditions associated with a sunset occurring in a clear atmosphere. In this case, it is caused by the temporary increase in the L-channel signal compared to the M-channel signal.

The source of the Purkinje Effect is the signal processing occurring within Stage 2 of the visual system. It can occur naturally within the mesopic region. It is an artifact of the logarithmic signal processing that results in the luminance signal (R-channel signal). The Effect cannot be observed under photopic conditions where color constancy is maintained.
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15.4.3.2.3 The problem with Wald’s absorption spectrum of the L–channel

The presence of the long wavelength artifacts found in the Bezold-Brucke and Purkinje Effects have had a significant and unexpected impact on the isolation of the long wavelength spectral channel of human vision. Figure 15.4.3-6 provides a caricature of the peak spectral wavelength in the luminance channel under transient conditions as a function of the ratio of M– to L–channel signal at the pedicles. Wald (unknowingly in the current context) used a transient technique to measure the peak wavelength of perceived brightness as a function of the ratio of M– to L–channel response. He did this by pre-adapting the M–channel using a bright flash. This suppressed the M–channel by a factor of about 100:1 relative to normal. As a result, he investigated the Purkinje region (peak wavelength 580 nm) under the impression he was exploring the L–channel dominant region (peak wavelength 625 nm). His erroneous proclamation that the L–channel peak of human vision was at 580 nm has been perpetuated to this day in the psychophysical community.

15.4.3.2.4 Definition of the unique Bezold and Purkinje illumination levels

These unique characteristics of the luminance response at the point of transition from the mesopic to the photopic regime and the similar transition from the photopic to the hyperopic regime allow an experimenter to define a specific luminance level that is characteristic of a particular human eye. This provides an absolute reference condition for that subject relative to illumination level that has been sought for a very long time. To observe these unique conditions, the luminous response must be measured using a narrowband light source, less than 10 nm. spectral halfwidth. The first unique illumination level occurs when the two relative peaks in the overall luminance response as a function of wavelength, in the region of longer wavelength than 532 nm., are of equal height. The natural illumination level resulting in this condition (and recognizable in Figure 15.4.3-6), will be labeled the Lₚ or Fₚ, for the Purkinje Illuminance. An auxiliary statement should be made concerning the spectral distribution of the radiant flux at this level. The second unique illumination level occurs when the two relative peaks in the overall luminance response as a function of wavelength, near 485 and 580 nm equal the height of the M–channel peak at 532 nm. This level, illustrated in Figure 15.4.3-5 will be labeled the Lₜ, for the Bezold Illuminance. Here again, a description of the spectral content of the illumination should accompany the value. An equal photon flux plot is most appropriate for these determinations.

15.4.3.2.4 Suppression of the M– and L–channels, the isolated S–channel spectrum

The theoretical treatment used in this model provides a very good explanation of some of the other data taken by

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Wald. He performed a series of tests to isolate the individual chromophores photometrically. By saturating the L-channel and the M-channel, he hoped to isolate the S-channel. Using this technique of saturating two out of the three channels, he could theoretically isolate all three chromophoric spectrums. However, the effect is transient and can only be observed for a short interval. Spectral sweeps proceeding from short to long wavelengths frequently give different results from sweeps proceeding from long to short wavelength. Figure 15.4.3-7 illustrates the very good agreement between some of his data and the theoretical absorption spectra predicted by this model. Note his data, indicated by the + symbols, does not exhibit transitions as sharp as those of the equations. His spectrometer had a bandwidth of about 30 nm, that was typical of the time period and accounts for most of the smoothing that causes the difference between the measured and the theoretical curves. Note the distinctly non-Gaussian flat top on the shape of the S-channel in this spectrum for both the theoretical and empirical curves. Similar, but less distinct, flat, non-Gaussian plateaus are seen in the region of 530-550 nm, and 590-630 nm. This is strong support for the proposed theoretical characteristics in Section XXX which are based on Fermi-Dirac statistics.

[[Note the flat top on the spectral absorption characteristic of the S-channel and the progressively narrower top on the characteristic for the M-channel and L-channel.]]

Figure 15.4.3-7 The S-channel absorption spectrum in humans, predicted by this theory (---) versus the measured data of Wald (+ +) for a yellow adapted photopic individual, R.H. Predicted spectrum based on $K_S=1000$, $K_M=9$ & $K_L=1.8$ and the edges of the absorption spectrums as shown in the Standard Eye of this work.
15.4.3.3 The perceived luminance threshold function under photopic conditions

15.4.3.4 The perceived luminance threshold response under scotopic conditions

Let the overall spectral response of the human eye be given by the same generic equation as developed in Section in 15.4.3.2:

\[
a'_{\lambda} = \log\left(k_s a_s(\lambda)\right) + \log\left(k_m a_m(\lambda)\right) + \log\left(k_l a_l(\lambda)\right)
\]

where the individual spectral responses remain those developed in Section 16.3.2 & 16.3.4. However, in this case, let the argument, \(k_{\lambda}\), of the last logarithm be equal or less than 0.1, making the last term negligible with respect to the other terms.

This overall spectral response is shown in Figure 15.4.3-8(a) and (b) and is the foundation of the C.I.E. Scotopic Luminosity Function. Note carefully that the peak response of this function has moved to a shorter wavelength than in the photopic function, a peak that is very near the peak of one of the underlying individual spectral responses.

It is important to note that the CIE 1961 Scotopic luminous efficiency function was obtained following the same dark adaptation protocol as the photopic standard.

Only the diameter of the stimulus field was actually changed, from two degrees to ten degrees.

15.4.3.5 The luminance response associated with the mesopic region

It is particularly difficult to discuss the human luminance threshold function without carefully describing both the magnitude and the spectral

![Image](image-url)
distribution of the stimulus throughout the period of interest. While natural illumination decreases greatly from around two hours before local sunset to astronomical sunset (1.2 hours after local sunset), its spectral content also varies widely depending on atmospheric conditions. A visible sunset is dominated by light in the long wavelength spectral region. This dominance tends to accentuate the Purkinje Effect. This Effect causes a peak in the perceived spectral response near 580 nm, a significant shift from the CIE stipulated peak at 555 nm. These two peaks are replaced by a CIE stipulated peak of 507 nm at one hour after astronomical sunset. The Purkinje Shift appears to be dominated by scattering of sunlight within the lower atmosphere. In the presence of heavy cloud within the lower atmosphere, the Effect is not observed.

Laboratory conditions are usually better controlled within the mesopic region than are natural conditions. However, they are frequently determined by a low color temperature incandescent light source and have generally been interpreted using a constant energy per unit wavelength criteria.

15.4.3.5.1 The nominal Mesopic threshold function

It is not necessary to treat the equations of Section 15.4.3.2 & 15.4.3.3 separately. By allowing the illumination level to vary over a wide range in the equation of Section 15.4.3.2, a series of spectra are obtained that can be plotted on one set of coordinates.
15.4.4 Perception of Color

15.4.4.1 Background based on the conventional wisdom

There is a great deal of discussion in the literature concerning the perception of color. A large percentage of it is contradictory at the detail level, particularly with regard to the absorption spectra of the L-channel. This is because of a situation similar to that concerning the perception of luminance;

- man’s penchant for thinking in terms of linear algebra and dichotomies
- most researchers have been comfortable using graphical templates for each individual chromatic channel.
- no comprehensive model has been available to illustrate the chrominance function.
- no theory has been presented based on a comprehensive model.

The problem of thinking in terms of linear concepts is highlighted in the recent paper by Lennie\(^{325}\). The discussion is based on the premise that the visual system is trichromatic at the smallest level of detail compatible with a triad of photoreceptors. However, he notes that the recent reports of Roorda & Williams does not support such orderly triads. Going further he defines a first puzzle regarding the wide range of ratios, between the putative ratio of M–channel to L–channel photoreceptors in the foveal area, between individuals. He defines a second puzzle with respect to the clumpiness of the photoreceptors associated with the individual channels, with large voids where no photoreceptors of a specific channel are found. He concludes that “the retinal circuitry thus seems to be haphazard in its dealings with L– and M– cones, yet its indiscriminate handling of their signals finds no expression in our color vision.” It is clear that his conceptual basis is not well aligned with the actual operations of the visual system. After some further musings, he concludes “Mechanisms in the cortex must therefore collect signals from many retinal inputs, thereby smoothing-out the local variations among them.”

This section will present a more realistic description of the perception of color by the visual system. It will also recognize the presence of ultraviolet photoreceptors in the human retina. The presence of these photoreceptors change the few statistics used in Lennie significantly.

\(\text{[[ I am not real happy with this paragraph ]]}\) This model has presented:

- the detailed equations for the absorption coefficients of each chromophoric channel,
- the fact that the L-channel is fundamentally different in the area of translation to an electrical signal,
- the fact that the fundamental signal in a neural signal is a current,
- the fact that the voltage associated with such current is related to it by an exponential function due to the load diode, and
- the presence of differential amplifiers among the horizontal and amercine cells which provide vernier signals that can be used to interpolate between ]].

The problem became complicated in the 1920-30’s when the C.I.E. sponsored a large effort to codify the practice of three-color Colorimetry. These activities sought to define a series of real primary colors that could be mixed together to create any other color. In this situation, the colors were assumed to be additive and the human eye was used as a null instrument. It was assumed that one of the principle parameters was energy and the tests were performed on an equal energy basis. The result was a set of color mixture curves wherein the long wavelength component actually went negative. Although the set of color mixture curves were shown to be linear homogeneous

combinations, they were difficult to work with. Therefore, the community defined a set of non-negative color mixture curves as well, based on the set of linear homogeneous combinations. Further complicating the matter was the fact that the middle wavelength component exhibited a spectrum that looked very similar to the (photopic) luminosity function that had just been adopted as a standard—a highly smoothed version of the mean of the test data collected by several different investigators. Therefore, the middle wavelength component was defined as equal to the luminosity function and a short and a long wavelength spectra were defined to meet the equal energy matching criteria. The resulting tristimulus values were totally theoretical and based on linear addition of components—however, they were all positive. Interestingly, and to this day, the long wavelength component has a significant relative maxima in the short wave spectral region.

All of the above manipulations were due to the use of a nonlinear color sensor, the human eye, as a presumed linear null detector. Subsequent mathematical manipulations have remain based on either equal energy or Planckian radiators, but always assuming linear homogeneous equations. These manipulations have resulted in a C.I.E. Chromaticity Diagram (1931) which has been adopted widely in industry but which has little relevance to the theory of vision; i.e., the peak wavelengths of the actual chromophores of animal vision do not occupy the corners—or any other recognizable location—on this diagram. The spectral capabilities of the so-called Standard Observer were derived based on the linear assumption.

Because of the above procedural problems, it is common for investigators to attempt to subtract the standardized short wavelength and medium wavelength human visual spectra from the C.I.E. standard photopic luminosity function in order to obtain the long wavelength spectra; the result frequently having a peak response in the region of 570 nm.

As noted by MacAdam, "Color differences consisting solely of chromaticity differences without luminance differences are rare, and there is no known way of evaluating the noticeability of combined luminance and chromaticity differences." This idea needs to be expanded a bit. The first clause is referring to the natural world. In the second clause, it might be better to replace the word "evaluating" with the word "separating" since there are experimental records that appear to measure the combined effects of luminance and chromaticity differences. The adaptation level in each chromophoric channel plays a major role in this area of measurement, as apparently do the exact chromophoric absorption characteristics.

As in the case of Section 15.4.3, this section starts from the basics;

+ the calculable absorption spectra of real chromophores based on the precursor, Vitamin A.
+ a model recognizing the non-linearity’s inherent in the visual process, especially in the L-channel.
+ the measured spectra of real in-vivo chromophores based on electrophysiological techniques.
+ the observable output of in-vivo spectral differencing circuits.

The data available in the literature can be fitted to the model used here with little difficulty. The visual process in animals utilizes up to four chromophores equally spaced with respect to wavelength as developed in Chapter 6. In humans, only three are used; the L-channel chromophore with a peak absorption at 625 nm., the M-channel chromophore with a peak at 532 nm., and the S-channel chromophore with a peak at 437 nm.—all plus or minus 2 nm. or less at body temperature. In the simplest chrominance path, each of these chromophores has a direct connection to the brain and the brain is able to perceive color based on its evaluation of the relative amplitude of these three signals. Although the L-channel translation process involves a square root function, the gain characteristic of the input activa of the photoreceptor cell tends to equalize the output of each channel at the axon of the photoreceptors, even in the presence of short term luminance changes of 10-100 to 1.

Large area

15.4.4.2 Fundamental sensation of chrominance

The fundamental sensation of chrominance is perceived by the brain based on the input signals from the three (four in many animals) spectral photoreceptor channels, the same three channels that are used to perceive luminance. Only in this case, the differences between various signal pairs is utilized instead of the sum of the channels.

15.4.4.2.1 Fundamental chrominance signals in the S and D pathways

There is the possibility of generating six pairs of difference signals in order to describe the chrominance of a given scene. There does not appear to be theoretical need for an actual difference channel in human vision involving the difference, S- minus L- or its complement. However, such signals are measured in zones V1, through V4 of the cortex (See the next Section). Whether such signals originate in the retina or are computed in the cortex is not clear. Experiments could be performed to answer this question by using an S- channel and an L-channel spectral light and seeking a difference signal in the plane of the amercine cells and/or the horizontal cells, the so-called region of the S-potentials. It also appears that the visual system relies on the differences S- minus M- and L- minus M-, and does not compute their complements. Here again the literature is not completely clear on this point. However, the circuit model used here would indicate that it would be awkward for the retina to calculate both the difference S- minus M- and M- minus S- pairs and maintain the necessary balance between the null points of each channel in order to avoid confusion (analogous to vertigo) at the higher cognitive levels. It appears that the long wave trichromatic animal utilizes only the two difference channels, S- minus M- and L- minus M- with the M-channel as the common node; while the short wave trichromatic animal uses the two difference channels, UV- minus S- and M- minus S- with the S- channel as the common node. Notice that S- minus M- is used in one group and M- minus S- is used in the other group. This situation elicits an interesting question that can probably only be answered by experiment; in tetrachromatic animals, what difference signals are actually used and how are the nodes treated? This may have a significant bearing on the best way to construct a research oriented chromaticity diagram.

To evaluate the differences enumerated above, it is important to note the three conditions illustrated in the model;

+ differencing takes place after the adaptation process is performed in each individual channel,

+ the amplification factor in the difference amplifier may be different for each channel, and

+ the polarity of the resulting difference signal is important since it appears that the signal is sensed at a voltage node in the brain.

The first condition accounts for the ability of the visual system to perceive a white level in nearly any scene regardless of the actual illumination spectrum. The second condition, if pathological, may be important in the definition of anomalous color vision. The third condition affects the overall linearity of the sensing process.

15.4.4.2.2 Unique chrominance capability of the S’ pathway

Based on the logarithmic summation and differencing associated with the S and D pathways, it is very difficult to decompose the signals received in the cortex via these pathways back into the unique spectra associated with photodetection. Only the difference signals between the S-, M- and L-channels have been found in the V1, V2 and
V3 zones. Zeki has described a more complex situation in zone V4\(^{327}\). In this zone, he has measured a group of difference signals as well as a group of signals that correspond to the original spectral characteristics of the chromophores. He noted that his data did not show a correlation in position within V4 to position within the retina. At the time of the paper, he considered the visual zones to be hierarchal in nature beginning with V1. He has since abandoned that view.

The paper is complex and can be divided into three separate experiments. In the paper, Zeki apparently used both a spectrometer for narrow band measurements and broad band filters. He probed V4 with a penetrating electrode. He did not specify the bandwidth of his spectrometer but measurements were reported with quite narrow half amplitude bandwidths. In the first experiment, his figure 1 clearly shows the presence of waveforms with spectral peaks at 438 ± 14 nm and 631± 14 nm and a waveform with a peak near 532 nm as well as some others. These three peaks are very close to the putative spectral peaks of the Rhodonines at body temperature in the macaque. The presence of these peaks in V4 is discussed below.

In the second experiment, he has also measured difference spectra in zone V4. These difference spectra could be described as exhibiting Hering like characteristics. This is because he selected the wavelengths to be used for excitation but only measured individual pairs of cells. Thus, he could measure the difference signal in the P-channel or the Q-channel but not both simultaneously. He appears to have measured a S- minus L- signal but this cannot be confirmed since he only measured one pair of cells. He could have been measuring the difference between a cell representing an S- minus M- signal (a P-channel) and another cell representing an M- minus L- signal (a Q-channel). He noted that none of his difference measurements went through the white point on the CIE Diagram (as expected by this work). See Section 17.3.3 for a more thorough discussion of these measurements using the New Chromaticity Diagram for Research.

The third experiment will not be addressed here. However, three broadband filters were used in conjunction with three “white” projection sources of unspecified color temperature. Lacking a detailed model of the visual system, he used a set of filters selected by Edwin Land. A sample of each was bound in the front matter of the publication. Although these filters appear to be gelatin based and do not represent the proper absorption spectrum shape, their center wavelengths were at 432 nm, 528 nm, and 660 nm (very close to the center wavelengths of the Rhodonines). Their peak absorption amplitude is also arbitrary.

15.4.4.2.1 Significance of the Zeki paper

The most important finding of the above paper was the presence of both chrominance difference signals and unprocessed photoreceptor output signals in zone V4. This zone does not exhibit spatial correlation with the retina. It is proposed that the difference signals arrived at this zone via the D pathway and V1 but the spectral signals arrived via the S’, or pulvinar pathway, probably via area 5 (not necessarily zone 5). This proposal is believed to be completely compatible with the post 1993 position of Zeki.

15.4.4.2.2 Explanation of the other waveforms in V4

Based on the above proposition, the other waveforms found in zone 4 could be calculated directly. Many of these waveforms are of narrow bandwidth but limited dynamic range. The basic model of this work would require extension to account for these waveforms in detail. Conceptually, this combination of difference and absolute spectral signals could contribute to additional reference points in the overall Chromaticity Diagram perceived by the visual system. With the absolute spectral signals available via a path independent of the logarithmic differencing channels, it becomes possible for the cortex to calculate principle points for the Chromaticity Diagram at the null points of the difference channels, i. e. 494 and 572 nm (the terminal points of the Hering axes). Although Zeki states he did not find any signal with a peak wavelength in the 560-570 nm region, he suggests this is not an exhaustive proof. It is possible he should have been looking for a negative going peak.

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15.4.4.2 Secondary sensation of chrominance

The fundamental sensation of chrominance is rather coarse. Therefore, the eye utilizes differencing circuits within the retina to provide a vernier measurement. The result is that the eye exhibits five (or possibly 6) reference points on the C.I.E. Chromaticity Diagram. The primary points associated with the peak wavelengths of the three chromophores at 625, 532 and 437 nm. and at least the two null points related to the differencing circuits at 572 and 494 nm. Whereas it is necessary to know the relative amplitude of the signals applied to the inputs of the differencing circuits and the relative gains associated with the inputs to the differencing circuits, it is clear that these circuits exhibit nulls in the vicinity mentioned. Values 595 and 495 nm. were given by Wright and Pitt for these quantities from behavioral tests with the human at body temperature. They did not specify the state of adaptation of the subjects.
Figure 15.4.4-1 shows the data points proposed by Hurvich And Jameson in 1955 to represent the CIE Standard Observer. The points resulted from data averaging after a measurement program and support the concept of this work that two orthogonal difference signals, S- minus M- and L- minus M-, operate as vernier signals that provide a fine level of discrimination. They show these two bipolar quantities as a continuum that they call the chromatic valence. Here, these two quantities will be considered separate (and in fact extendible to include a third difference signal, UV- minus S-) as a New Chromatic Diagram for Research is presented. This work will show the null values in this figure are determined by the state of adaptation of the eye.

15.4.4.3 Just noticeable spectral differences

Wright & Pitt have provided a curve of just noticeable spectral differences, using only 5 individuals, that has stood the test of time. It appears that they provided a man made test signal that did provide a chromaticity difference without a luminance difference at the cornea. However, the absorption characteristics of the individual chromophoric channels may have still played a part. They only provided a smoothed curve, no data points or error bars. Their data shows two minima, at about 495 nm. and about 595 nm. which are where they would be expected from the model developed here. However, taking the absolute values of the derivatives of the S-M channel and the L-M channel using the absorption characteristic half amplitude points for the constant Q=4.8 version of this model do not provide minima of the same relative magnitude as seen in Wright & Pitt’s data. The difference is about 2:1. Alternately, using the half amplitude points associated with the equal spectral absorption intervals for each chromophore, this difference in magnitude can be reduced but with the maxima between the two minima still too large. Comparing the details of the model with the data from Wright & Pitt may allow the half-amplitude absorption characteristics of each chromophore to be established to a very high degree of accuracy. Additionally, these anomalies may be due to the difference in the absorption cross-sections of the different chromophore channels in the retina and/or differences in amplifier gain in the various neural circuits behind each photoreceptor. Further experiment may help resolve this problem.

15.4.4.4 Chromatic inference

As discussed in Section 14.7.XXX, the suite of signals sent to the brain can be decoded in different ways depending on the time delay related to the initial luminance signal. In the absence of a luminance signal however, there appears to be no way to insure the proper decoding of the chrominance signal. The brain must then infer, from

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the surrounding area in the database, the most likely chrominance value for the image at that point. Yarbus\textsuperscript{330} has demonstrated that this is the case in an extensive series of experiments. By using only one eye and establishing an “empty image field”, the subject reports the field as going dark, typically after 1-3 seconds. If a colored border is created around the empty field, the subject will report that the empty field has taken on the color of the border. If the border is changed to a checkered field, the empty field does not change to the color of either checker but remains a null gray. This indicates that the brain will infer a color for any image space surrounded by a single color. If the surround is not of uniform color, the brain will look for other clues as to the best estimate of the regions proper color or continue to report an empty field of null gray.

15.4.4.5 Chrominance as a function of angular field

Wyszecki & Stiles\textsuperscript{331} provide an interesting discussion of the effect of angular field on the perception of color. They point out that much of the research, particularly regarding perceptual color defects, has been carried out using small centrally located fields of view, 1-2 degrees centered on the fovea; and that when larger fields are used, different results are often obtained. Specifically, many subjects respond as dichromats when tests are performed using very small field angles but respond as normal trichromats when larger test fields are used. Wald provided a caricature of the color performance of humans versus field angle. He described the color-normal human as being blue-blind within a 1/8° radius of the fixation point, a trichromat out to a radius of 20-30°, a red-green dichromat from there to 70-80° and a monochromat beyond that region.\textsuperscript{332}

15.4.4.6 Illustrating the perceived color space

As discussed above, the visual system employs chromatic signals that are rectilinear and orthogonal to each other. There is no indication in the literature that the brain employs any radial coordinate system or is capable of performing the mathematical transformations that would be required to use such a system. It appears that the brain employs a two (or three) dimensional lookup table to determine the color of a scene element for purposes of reporting its response to a stimulus. This fact need not impede the intellectual part of man from representing the color space in radial coordinates for his intellectual pursuits separate from his operational activities.

15.4.4.6.1 The current Chromaticity Diagram

The current set of C.I.E. Chromaticity Diagrams are an entirely empirically derived set of presentations that make no claim to being based on the chromophores of vision. They were derived from an intellectual exercise based on the following assumptions;

+ that color mixing in the physical world was additive.

+ that the human eye was a good quality null detector that could be used to determine the chromatic equivalence of two different color mixtures.

+ that the human eye exhibited a uniform sensitivity to light over the range of the colors used in the color mixtures (independent of illumination level as long as the level was in the (undefined) photopic range.

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The last assumption is clearly not appropriate for research quality work although it is adequate for most commercial and engineering purposes; and the human eye is known to exhibit a variation (albeit relatively small—on the order of 2:1 in the middle spectral range) in sensitivity to color differences that varies over the spectral band of the eye.

15.4.4.6.2 Candidate chromaticity diagrams

Based on the model developed here, it is possible to define a number of chromaticity diagrams that might be of greater value in the research community and in the evaluation of color vision abnormalities. Some of these diagrams offer a higher degree of accuracy, simpler experimental verification, and a more rational relationship to the underlying processes than do the C.I.E. equivalents. One presentation offering considerable merit is developed below.

Candidate A  [[[probably not useful xxx]]]

Assuming for the moment that the overall amplification factors for each of the chrominance signals are the same as measured after the differencing process*; if the two signal differences that are used in the chrominance channels of human vision are normalized with respect to the common node, M-, (S- minus M-)/M- = S-/M- minus 1 and (L- minus M-)/M- = L-/M- minus 1, two orthogonal functions are obtained that can be easily plotted to form a theoretically oriented (and hopefully research oriented) chromaticity diagram. Note that the values of S-, — and L- are necessarily positive in this analysis; the differences range from 0 to -1.0. Since these two functions are mathematically orthogonal, it is logical to plot them along perpendicular axes. [[[ Insert figure XXX if this section is used]]]

Candidate B, applicable two trichromats using the long wavelength triad of chromophores  [[[appears quite useful xxx]]]

Assuming for the moment that the overall amplification factors for each of the chrominance signals are the same as measured after the differencing process*; if each channel is normalized in terms of this amplification factor, the difference signals, S- minus — and L- minus — will each exhibit a range of -1.0 to 1.0. The parameters S- minus M- and L- minus M- are mathematically orthogonal to each other, although they contain a common node, M-. Since these two functions are mathematically orthogonal, it is logical to plot them along perpendicular axes. The result is shown in Figure 15.4.4-2 Figure XXX(a). This plot provides a rectilinear presentation of a chrominance diagram at a given level of illumination under equal channel gain conditions, preferably relative to a specific illumination level and an illumination environment that is described by the equal photon flux per unit wavelength criteria (8,000 K color temperature if the UV is included, otherwise 7053 K color temperature) but acceptable under other illumination level and color temperature environments as long as they are specified. Furthermore, the common node, (-1,-1) occurs at 532 nm. in the ideal case where the absorption spectra of the chromophores does not overlap at all; spectral S-, defined as 437 nm. occurs at the abscissa value of 1.0 and spectral L-, defines as 625 nm. occurs at the ordinate value of 1.0 also. All spectral colors lie along the axes. The coordinate 1,1 is the purple point corresponding to the point complementary to 532 nm. and normally written as 532C nm.

* A condition that is only possible for a very limited range of illumination due to the variability of the L-channel gain with illumination.
* A condition that is only possible for a very limited range of illumination due to the variability of the L-channel gain with illumination.
The null value along each axis corresponds to the condition where the two signals are of equal amplitude at the output of the differencing circuit, and presumably, (for the moment at least) at the output of the cognitive circuits in the brain. This provides a definition of white that is very similar to the system used in NTSC color television where the two chrominance signals disappear when the system is transmitting a “white” scene. In vision, the sensation of trichromatic white corresponds to the condition where, after adaptation, the two chrominance signal channels exhibit a “zero” value as sensed by the higher cognitive centers. This zero value may be more properly defined as a null condition in vision, i.e., where the sensation of color related to a scene or scene element is undefined. This null condition could be described as a zero saturation condition, regardless of hue value.

Note that this chromaticity diagram involves two orthogonal parameters, but they share a common node. Under this set of conditions, it is possible to define an arbitrary set of orthogonal axes centered on the trichromatic white to aid in the quantification of hue. However, none of these axes will be strictly compatible with the axes envisioned in the recent expositions of the Opponent Theory based on the C.I.E. Chromaticity Diagram. On the other hand, the NTSC Color Television Standard is based on this very same concept of color signal differencing; see section XXX. It has been found economically useful to build color television receivers based on either of two sets of axes overlaid on the diagram developed here. These axes are known as the XXX and XXX.

Using the above trichromatic chromaticity diagram format based on the long wavelength triad of chromophoric channels, Rhodonine 5, 7, & 9; it is possible to extend this concept in a number of ways;

+ to provide a similar diagram for the trichromats using the short wavelength triad of chromophoric channels (assumed to be all protostomia).

+ to provide a similar diagram for all tetrachromats.

+ to provide a graphical description of the various abnormalities of color vision

Candidate B, applicable to trichromats using the short wavelength triad of chromophores

Figure 15.4.4-3 Figure XXX(b) illustrates the similar diagram for trichromats utilizing the short wavelength triad of chromophoric channels, Rhodonine 7, 9, & 11. In this case, white is defined in the same manner as in (a) but occurs in the region that could be described as one-half way between UV- and M-, essentially at a point defined by the intersection of diagonal lines drawn across the square. This intersection could be described as at the midpoint of the line drawn between 437 nm., 437C nm.
Candidate B, applicable to tetrachromats using the complete gamut of chromophores

Figure 15.4.4-4 Figure XXX+1 describes the extension of this concept to include tetrachromats. A three dimensional view is shown as the most accurate presentation preserving the orthogonality (in this case represented by the perpendicularity) between the various difference signals. By analogy with the earlier trichromatic presentations, white is clearly represented by the point in three dimensional space where all three difference signals are at numerical zero; the result is that all of the chrominance sensors in the brain report a null condition—all chrominance information vanishes and the scene is perceived as “white”. It would be interesting to expand the preliminary probative work of Gaydon\(^{12}\) as to how a tetrachromat describes the condition of “white”; he asked some interesting questions to a few aphasics that bear on this subject, but not enough questions or under suitable test conditions. (see section XXX.)

15.4.5 Similarity to closely related technologies

15.4.5.1 Significance of parameters to NTSC Color Television standards

When color television was developed, there were many possible methods of sensing encoding, transmitting, decoding and displaying the necessary signals. One of the criteria forced on the industry by the U.S. Federal Communications Commission was to use as small an overall bandwidth as possible, preferably no more than for the then extant black and white system. This caused the industry to mount a major effort to discover the engineering parameters of the human visual system, through extensive psychophysical testing focusing on an acceptable level of re-creation of the original image. The tests ultimately included side by side comparison of the real and re-created images with the re-created image subjected to a variety of surround illuminations. The principle finding were that;

\(^{12}\)Gaydon, A. (1938) see below/ or above
the human eye did not perceive hue or saturation changes related to color in fine details of an image.

the eye was much more sensitive to changes in the yellow-green region of the spectrum than in either the orange-red or the purple-blue regions, especially in spatial regions involving a sharp change in luminance.

the linearity of the overall system must be quite good in the middle range of illuminance for a given picture.

These facts led to the final definition of a system that transmitted the luminance component (containing primarily the yellow-green information) at the maximum temporal bandwidth available, corresponding to maximum spatial resolution; a chrominance signal containing two components corresponding to a set of axes drawn as an overlay on the research chromaticity diagram developed here and with 0.0 centered on the trichromatic white point. Since the television system necessarily involved a sampling process, it was important to minimize the interference due to the sampling process. By selecting the axes of the chrominance channels as indicated above, and using a sophisticated form of subcarrier modulation, the system transmitted no chrominance information whatever, not even an unmodulated subcarrier, when presenting a white portion of a scene.

To maximize the utility of the amplitude spectrum available, the system was designed to compress the dynamic range of the signal to be transmitted, introducing a gamma of 0.5 in each color sensing channel prior to encoding, and to expand the signal after decoding at the receiver, using a gamma of 2.2 in the display device.

15.4.5.1.1 Visual signals to NTSC Color Television signals

As indicated above, The NTSC Color Television Standard is based on the very same concept of color signal differencing as proposed for the candidate research chromaticity diagram; see section XXX. It also transmitted the luminance information over a separate channel from the chrominance information. To maintain realistic, and acceptable, flesh-tones in particular, it was found necessary to very carefully specify the linearity and dynamic range of the various signal channels. Figure 15.4.5-1 illustrates the prescribed axes for use in NTSC Color Television overlaid on the proposed research chromaticity diagram. [[see ITT handbook pg. 796]]

As an interesting sidebar, it has been found economically useful to build color television receivers based on either of two sets of axes overlaid on the chromaticity diagram developed here. One design uses axes parallel to the S- minus — and L- minus — axes. This design recreates the three primary color signals usually described as R, G, & B in the television trade, but not the same as R, G, & B of the visual sciences. The second design recognizes that an axis passing through the — node represents a signal very similar to the luminance portion of the overall signal. Therefore, it senses only one chrominance signal along the S- minus L- axis and combines that signal with the luminance signal to compute the S-, — and L- signals, a saving of a few percent in terms of total cost for the resulting receiver. These two designs are described in television-ese as using the I-Q axes in high quality sets and using the Y-XXX axes in the cheaper sets. [[ITT handbook only gives Y, I-Q set]] Figure 15.4.5.2-1 also shows this less optimum set of axes.

15.4.5.1.2 Similarity of Visual and NTSC signal

For purposes of signaling, it is remarkable how closely the NTSC signaling system matches the animal signaling system. Both systems employ a series of spectrally independent but overlapping photo-sensitive sensors. The data from these sensors is separated into separate luminance and chrominance paths. The signal processing differs between the two based on man’s state of the electronic art in the 1950's and the need to maintain a simple topology in animal systems. The NTSC luminance path is treated somewhat simpler than the animal equivalent. Since

* See the color spectrum of the color television display devices in section XXX
television is a reproduction system, the luminance channel strives to maintain a linear end-to-end transfer function. Furthermore, the use of logarithmic circuits by man was unusual in the 1950's. This led man to build circuits that performed linear algebra and then use a single logarithmic amplifier, gamma = 0.5, prior to transmission of the signal. At the receiver, the naturally logarithmic characteristic of a triode was used as an inverse logarithmic amplifier, gamma = 2.2. On the other hand, suppressed carrier encoding for purposes of signal transmission (projection) was easy for the NTSC and is difficult in an animal system. The suppression of the chrominance channel carrier in the absence of chromatic information avoids many cross-talk problems in the NTSC system. A similar elimination of “action potentials” in the chrominance channels in the absence of color information in animals would eliminate many of the transient flicker effects observed in human vision.

One of the principles in the development of the NTSC Standard was Otto Schade of RCA. Later, he wrote several academic papers regarding vision. He presented one of the earliest computational models of human vision using a tri-color television camera chain as an analog.13

15.4.5.2 Simplicity of Initial Perception to “Paint” programs

It is instructive to compare the perception of luminance and chrominance in the human eye with a family of computer programs generally described as paint programs. In a graphic computer program, you can select any region enclosed by some feature(s) and tell the computer to “fill” that region with a color or a brightness level of your choice. In the case of the eye, there is no higher power to make such a choice so it does one of two things:

+ If the enclosure is surrounded by a uniform chrominance or luminance, the brain will assign that value to the entire enclosed region.

+ If the enclosure is not surrounded by a uniform chrominance or luminance, the brain will refrain from filling the enclosed region, leaving it a null gray, and it will seek other clues, such as from memory or from another eye with an overlapping field where available. When it locates a credible value, it will fill the region with this value.

Ditchburn14 has indicated how important this function is in vision; pointing out that it is used to compensate for the blind spot of the eye, for various small scotomas of the retina that occur during life, and for the larger blood vessels laying in the optical path but spatially stable relative to the photoreceptors of the retina.

15.4.5.2.1 Parameters used in the biological paint program

\[
\begin{array}{|c|c|c|}
\hline
\text{color} & \text{x} & \text{y} \\
\hline
\text{Red (R)} & 0.61 & 0.33 \\
\text{Green (G)} & 0.21 & 0.71 \\
\text{Blue (B)} & 0.14 & 0.08 \\
\hline
\end{array}
\]

Figure 15.4.5-1 The NTSC color signal axes and reference burst overlayed on the New Chromaticity Diagram Incomplete, see text.

Understanding how the brain implements a paint program in vision is complicated by the tremor of the eye. The brain generates the open loop tremor signal that drives the motor neurons of the ocular muscles. It establishes a reference time with respect to these drive signals and correlates the resulting visual signals with this reference. The absolute location of an element in object space is determined by the arrival time of the first pulse in a luminance response relative to the reference. The relative amplitude of that response, compared to adjacent elements in object space, is derived from the train of pulses following the initial pulse. In the above discussion and the next paragraph, the brain does not actually measure time intervals. It measures the phase of a signal relative to a full period of the repetitive pulses in the tremor signal.

In order to determine the hue of the color to be assigned to a given area in object space, the brain attempts to follow the same procedure in chrominance signal space as it uses in luminance signal space. There is a problem however. The chrominance signals are not synchronized with the tremor drive signals. The two chrominance signals involve the phase modulation of two continuous frequency oscillator. Using the arrival time of the first pulse in either or both chrominance signals relative to the tremor pulse leads to spurious information. However, by demodulating, low pass filtering and finding the amplitude ratio between the two chrominance data streams, a true calculation can be made for both hue and saturation. This is the procedure actually employed under normal conditions.

The brain takes the above luminance, hue and saturation values relative to a series of points along the periphery of a contour and processes these values in order to assign a nominal (and uniform) luminance, hue and saturation value to all points within the contour.

Many of the unusual flicker effects recorded in the literature involve the changing of the object space content in less time than required by the low pass filter circuit to determine an actual hue, and frequently less time than required by the luminance channel to determine an actual luminance level. If the change is so fast that it interferes with the luminance calculation, a contrast reversal is frequently obtained. Otherwise, only an assortment of spurious hues are perceived.

15.4.5.3 Similarity of perception to “colorizing” old movies

Recently, the colorizing of old movies has become quite popular and economically feasible on a large scale. The process is very similar to the “paint” process described above. It uses a sophisticated television scanner to scan the raw film record, the computer logic determines regions of fine detail and regions of less detail in each frame of the imagery based only on luminance information. It then asks a human operator to specify the hue and saturation of each region of the scene. Fortunately, these parameters do not change too rapidly from frame to frame and the computer is able to use the same values for a number of frames before requesting conformation of the values to use in subsequent frames. Perception involves the same procedure, recreation of the overall scene based on the information provided by the luminance channel and then the introduction of hue and saturation information from the signals recovered from the chrominance channels.

15.4.5.4 Similarity of perception to digital compression of television

Modern encoding of television signals for transmission over limited bandwidth facilities are found to use techniques very similar to those of the human eye, except modified to account for the raster scanning utilized in broadcast television. The details are very involved; however, the concepts used are straightforward. Basically, the encoder differentiates between regions of fine detail and regions of continuous luminance and/or chrominance. It encodes these areas separately using much the same techniques as outlined above.

At the point of decoding, the decoder uses the information received almost exactly as the brain does; the signals associated with each frame are decoded to define the regions of fine detail and the regions of less fine detail in each frame; and it defines the major “edges” in the overall scene. It then re-creates the regions of fine detail using a
single chrominance value specified in the signal and a run length encoded luminance signal. In regions of less fine
detail, the re-created signal is filled in using a paint program based on luminance, hue and saturation signals
transmitted separately as digital words. More sophisticated systems may use various preprogrammed ramp functions
to fill in areas more exactly and avoid contour lines; similar to the processes of cognition in the higher cognitive
centers of the brain.

To make this process even more efficient, the computer performing the decoding remembers the cues applied to the
previous frame; therefore, it is only necessary to transmit the differences in the cues between adjacent frames of
imagery. A high degree of compression can be achieved in this way, however, the process is memory intensive.
When a scene changes suddenly, nearly a complete frame of detailed information must be transmitted before
reconstruction of the next frame of imagery can begin. To avoid, the presentation being stopped while awaiting this
detailed information, it is necessary to provide a large temporary memory to buffer the information going to the
display device.

A process very similar to the above process is used in the brain to maintain a perception of a high quality wide angle
scene even though the fovea of the eye is only able to collect details from a small area of the overall scene at a given
time and thereby sequentially update the overall perceived image. The visual process is also memory intensive.

15.4.6 Causes of abnormalities in human perception related to the CNS

The human visual system is subject to a number of errors. Many of these are found in the eye itself. Others are
found in the CNS. Errors can also be introduced by the surgeon (infrequent) and through accident. Categorization
of the source and functional nature of these errors can aid in the further understanding of the visual system. The
phenomenology and performance degradation associated with these errors is addressed in Chapter 18.

15.4.6.1 Abnormalities related to color EDIT

15.4.6.1.1 Misperception in the normal human eye

The errors associated with the normal eye are generally inconsequential when viewing the natural environment. The
presence and consequences of these error becomes more significant when faced with the man-made environment of
rapidly moving objects, short temporal duration luminance changes, non-Planckian light sources, etc. The problems
and the results of mis-perception can best be characterized as due to the employment of a sub-system, the human
visual system, outside the scope of its design specification. Many of the results of these misperceptions are lumped
under the category of optical illusions. The field of exploiting the misperceptions of the normal human eye plays a
major part in the technology known as Magic. Many other misperceptions are of minor importance and are
generally listed in the scientific literature as “phenomenon” associated with an investigators name.

15.4.6.1.1.1 Errors in color rendition.

Many optical illusions are related to the perception of color while viewing a rotating, or otherwise moving, black and
white image element. As indicated in Section 14.6.2.1, if an image is presented to the eye that causes an unexpected
state related to the signal vector, particularly the timing of the initial luminance pulse received from a ganglion cell,
the eye may report a chrominance value which is erroneous.

[[ xxx discuss again the errors in reading the data vector associated with a given visual zone , chap 14.6.2.1, which
results in perceiving color in a rotating wheel with a black and white pattern on it. relate it to the herring bone
pattern problem of NTSC color television which generates a rainbow pattern at an angle to the herring bone weave.

15.4.6.1.2 Misperception in the abnormal human eye

15.4.6.1.2.1 Errors in color rendition
Because this is a very old field of scientific investigation, there are significant difficulties and conflicts with regard to the definition of terms. Deuteranopia is a good example. Early investigators defined three fundamental types of color abnormality related to the detection process and based on the use of Greek roots; protanopia for the loss of the “red” photoreceptor, deuteranopia for the loss of the “green” and tritanopia for the loss of the “blue”. The loss of the “green” photoreceptor was never confirmed and the term was redefined to indicate a secondary type of color abnormality related to the signal differencing function, deuteranopia became the name for a failure in the “red” minus “green” channel. Based on symmetry considerations, Mueller defined a new term in 1924, tetartanopia, to describe a failure in the “blue” minus “yellow” channel, clearly relating to the opponent theory of color vision. Using the terminology of this work, where the initial sensing only involves three chromophoric channels, deuteranopia indicates a failure of the L- minus M-channel and tetartanopia indicates a failure in the S- minus M-channel. Under this model, it is quite possible there is a fifth abnormality, tentatively christened pentanopia and indicating a failure in the S- minus L- channel. It appears that failures of the tetartanopic and pentanopic (if any) types are not as obvious and important in modern life as failures of the deuteranopic type. Following Mueller’s logic, it is also quite possible that there is a color vision abnormality in insects related to the UV- minus S-channel which for completeness and symmetry will be called hexanopia. Table 15.4.6-1 summarizes and helps visualize the significance of these names.
Table 15.4.6-1

Classification of failures in the tetrachromatic visual system

<table>
<thead>
<tr>
<th>Protanopia</th>
<th>Loss of L-channel</th>
</tr>
</thead>
<tbody>
<tr>
<td>(unnamed)**</td>
<td>Loss of M-channel</td>
</tr>
<tr>
<td>Tritanopia</td>
<td>Loss of S-channel</td>
</tr>
<tr>
<td>Pentanopia ?</td>
<td>Loss of UV-channel</td>
</tr>
</tbody>
</table>

Deuteranopia      Loss of |L- minus M-channel|
Tetartanopia      Loss of |S- minus M-channel|
Hexanopia ?       Loss of [UV- minus S-channel|

** This term has not been named in recent times, probably because of two things; 1) most visual deficiencies are gauged against the performance of the M-channel, and 2) it appears that total loss of only the M-channel, if it occurs, is usually equated to blindness without regard to color performance.

? Pentanopia and Hexanopia will probably remain of only theoretical interest unless some investigator isolates one or both of these conditions (in insects) and begins to trace some genetic cause for them.

The losses shown on the right in this table are shown within absolute brackets at least until more definitive work can determine what sign is appropriate for each term or whether both differences are present in a given animal.

The deuterastomic species exhibiting trichromatic vision will not normally exhibit sensitivity in the UV or a difference signal related to the UV- minus S-channel. Only further work will determine explicitly whether the Aphakic human exhibits one or both of these channels.

Besides the generally inconsequential errors in color rendition of the normal human eye, there are a broad range of more serious errors in color rendition associated with the term color blindness, or more precisely anomalous color vision. Utilizing this model in its complete form, it is possible to characterize these errors explicitly, with a greater degree of precision and with a higher degree of specificity with regard to their cause. Table 15.4.6.1 provides a first level matrix of these errors and their cause. Because of the great importance of sex in discussing the occurrence of the different color abnormalities, the frequencies given in this table are for males; other values for females will be given in the text.

Table 15.4.6-2 will indicate some of these problems by utilizing both a formal name and an informal name for some classifications. There is also a common problem of using the adjective form of a word (dichromatism) to describe one set of conditions while using the noun form (dichromat) to describe a different specific situation. These differences and difficulties will be discussed further below. However, in this work, a clear distinction will be made between;

+ a *structural* dichromat as one who only has two fully operational luminance signaling channels.

+ a *functional* dichromat as one who can match any color seen by a normal trichromat using only two independent monochromatic stimuli.

In addition, there has been a tendency to separate a weakness with regard to a given chromatic abnormality from a complete failure of this same abnormality. A complete failure of a luminance or chrominance channel in an animal visual system appears to be a rarity. However, the practice has arisen in all cases of defining (as an example) a
protan as a class containing both protanomaly, a weakness in sensing in, and protanopia, a total loss of sensing in the “red” channel.

There has also been a practice of defining these conditions with regard to colloquial color names that are not tied directly to the color spectrum, a situation that leads to scientific confusion; particularly since “blue” and “green” are not directly related to the dominant color of the visual chromophores, and even “red” is not adequately descriptive of the L-chromophore. Recall that, using this model, the peak response of the S-channel chromophore is most accurately associated with Purple (437 nm), the M-channel with Yellowish-Green (532 nm) and the L-channel with Orangish-Red (625 nm). Other perceived colors are based on computation within the signal processing system of the retina/brain.

A greater difficulty in the study of abnormal color responses has been the reliance on the putative linearity of the human visual system and the also putative definitions of \( r(\lambda) \), \( g(\lambda) \) and \( b(\lambda) \) in one form or another. This has necessarily skewed the discussion to imply the erroneous; that red, green and blue are the primaries used in the human visual system and that the chromophores of vision have peak sensitivities at 445, 545 & 605 nm. Much of the data has been collected from a variety of different investigators; thus, it is virtually impossible to assure that they all used the same illumination level in their measurements and avoided variations in their luminous efficiency and spectral analyses due to the Bezold-Brucke phenomenon.

Wyszecki & Stiles\(^1\) have provided considerable raw data and references from which a more detailed understanding of these abnormalities can be obtained. However, the assumptions of linearity and the importance of “red”, “green” and “blue” must be avoided; many of their assertions are dependent on these assumptions. And, most of their calculations are based on the linearity assumption, even to the use of linear matrix algebra. In addition, the wavelengths of the maximums in the luminous efficiency curves for all abnormalities, except for the true protanope, are all within the normal subjects variability in this parameter, given by Wyszecki & Stiles on page 396, 549 to 570 nm. Whereas their table 1(5.14.2) includes a line indicating shortening of the red (i.e., reduced luminous efficiency of long wavelength) in the case of protanopia and protanomaly, they do not include a line indicate a shortening of the blue for the case of tritanopia and tritanomaly.

TABLE 15.4.6-2

First Level Matrix of Misperceptions of Color in the Abnormal Eye*

<table>
<thead>
<tr>
<th>Formal Name</th>
<th>Informal Name</th>
<th>Freq.</th>
<th>Primary Trait</th>
<th>Prob. Locat.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Achromatopsia</td>
<td>Monochromatism</td>
<td>0.003%</td>
<td>Lack of all signal differencing and/or</td>
<td>Lack of L-chromophores Photoreceptors</td>
</tr>
<tr>
<td>2. Atyp. Achromatopsia</td>
<td>Dichromatism</td>
<td>2-3%</td>
<td>Lack of differential output</td>
<td>Amercine Cells</td>
</tr>
<tr>
<td>3. Protanopia</td>
<td>Anom. Trichromatism</td>
<td>5-6%</td>
<td>Abnormal differ. output</td>
<td>Amercine Cells</td>
</tr>
<tr>
<td>4. Protanomaly</td>
<td></td>
<td>1%</td>
<td>Lack of L-chromophores</td>
<td></td>
</tr>
<tr>
<td>5. Deuteranopia</td>
<td>Green blindness</td>
<td>1%</td>
<td>Reduced L- sensitivity</td>
<td></td>
</tr>
<tr>
<td>6. Deuteranomaly</td>
<td></td>
<td>1%</td>
<td>Lack of — minus L- output</td>
<td></td>
</tr>
<tr>
<td>7. Tritanopia</td>
<td></td>
<td>5%</td>
<td>Reduced — sensitivity</td>
<td></td>
</tr>
<tr>
<td>8. Tritanomaly</td>
<td></td>
<td></td>
<td>Lack of S-chromophores</td>
<td>Photoreceptors</td>
</tr>
<tr>
<td>9. Tetartanopia</td>
<td></td>
<td>rare</td>
<td>Lack of S- minus L- output</td>
<td>(Normal luminosity curve)</td>
</tr>
<tr>
<td>10. Acquired conditions</td>
<td></td>
<td></td>
<td>Due to disease, vitamin deficiencies or drugs</td>
<td></td>
</tr>
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</table>

* Table based primarily on text in The Science of Color, pages 134-139

15.4.6.1.3 Genetic basis for abnormal visual function

Many of the genetic aspects of abnormal color vision have been recognized for a very long time, including the fact that the anomaly is passed primarily down the male line and it has a habit of skipping generations. Boynton16 and Pokorny, et. al.17 provides considerable discussion of these characteristics.

15.4.6.1.3.1 Abnormals missing one of the three normal chromophores

It is generally recognized that a true protanope (3) exhibits a scotopic luminous efficiency function at all illumination levels, i.e., under psychophysical conditions their luminous response does not indicate the presence of any L-channel chromophores. Thus, the true protanope is a structural dichromat, exhibiting only two chromophoric signaling channels. Deuteranopes (5) on the other hand exhibit normal photopic and scotopic luminous responses. Clearly, there is a defining difference between these two types who both indicate difficulty in distinguishing “reds” from “greens”. The difference is that the protanope is not employing a L-channel chromophore at all while the deuteranope is employing an L-channel chromophore in a fully structural chromophore (luminance) signaling channel. The failure in a deuteranope is due to his inability to perceive properly the difference between wavelengths intermediate between the peak wavelengths of the L-channel and the M-channel, a failure in the M- minus L-(chrominance) channel. A deuteranope can accurately be described as unable to differentiate red from green and is therefore a functional dichromat requiring only a mixture of two independent stimuli to match any color recognizable by a normal trichromat. This failure can be due to a failure in the americine cells of Stage 2B, a failure in the Stage 3 midget ganglion cells, or in a failure in Stage 4—the decoding circuitry of the brain. It may be possible to ascertain if it is an americine cell failure in-vivo by careful testing using ERG techniques.

The tritanope (7) exhibits a condition analogous to the protanope (3), under psychophysical conditions, the luminous

---

response of the tritanope indicates the in-operability of the S-chromophoric channel. This is difficult to observe in the luminosity function because the S-channel plays a minor role in this overall response. The subject exhibits normal photopic and scotopic luminosity functions except for a decrease in the amplitude of both responses at wavelengths shorter than 500 nm. and no inflection points near 450 nm. or 480 nm. A heavily smoothed spectral response for a Tritanope should show a slightly longer peak wavelength than in the normal photopic luminosity function; however, the variability of this peak among individuals is greater than the difference anticipated between tritanopes and normals. The tritanope is a structural dichromat and exhibits the characteristics of a functional dichromat. This defect is easily detected by measuring the photopic luminosity function with a monochrometer of less than +/- 5 nm. bandwidth and under conditions of selective chromatic adaptation, i.e. yellow adapted conditions.

The analogy between the protanope and the tritanope is clearly seen if lines of constant dichromatic chromaticity are drawn for each of these types on a C.I.E. 1931 Chromaticity Diagram. The lines converge at the wavelength of the missing chromophore. A similar plot for the deuteranope is basically different; it consists of a set of equally spaced lines that are parallel to the line connecting the peak wavelengths of the L- and — chromophores. See Wyszecki & Stiles figure 1(15.14.2). Based on this fundamental difference, it is possible to say categorically that the deuteranope is not a structural dichromat in the sense of only employing two chromophores in its visual system. It remains a functional dichromat, however, in the sense of only requiring two independent color stimuli to match all color stimuli recognized by the normal trichromat.

An overall review of the literature would indicate that there are very few true and absolute structural dichromats; those exhibiting a complete failure in one of the three fundamental chromophoric (luminance) channels of human vision. There are, however, a variety of subjects exhibiting a restricted ability to perceive color differences to the level of the majority of the population. These subjects constitute a large class ranging from the slightly impaired anomalous trichromats to the more severely impaired functional dichromats incapable of differentiating between reds and greens (the deuteranomalous, lacking the chrominance channel that provides the M- minus L- signal), between purples and greens (the tetartanomalous, lacking the channel that provides the M- minus S- signal), and possibly between the blues and reds (the pentanomalous, lacking the channel that provides the S- minus L- signal, if normally present). There is some question as to whether the S- minus L- signal is even computed in the retina and sent to the brain. There is little doubt that the — minus S- signal is computed and sent to the brain but this difference is associated with an area of the photopic function that is perceptually less significant than that of the — minus L- signal.

The slightly impaired anomalous trichromats and functional dichromats may only involve an abnormality in the gain of one of the channels input to the amercine cells, an inappropriate nominal time delay in the output of the midget ganglion cell, or in the threshold of the decoding circuit in the brain associated with that chrominance channel.

15.4.6.1.3.2 Abnormals missing two of the three normal chromophores

Although exceedingly rare, there are reports of structural monochromats. Blackwell & Blackwell\(^\text{18}\) report cases where the retinal response is limited to a chromophore with maximum response at about 440 nm. Wyszecki & Stiles discuss in general a category of monochromats with a peak spectral sensitivity at about 510 nm. However, unless an absorption spectra was obtained for these individuals using a monochrometer with a bandwidth of less than +/- 5 nm., the structural failure of the S-channel can not be easily confirmed. It is more likely that these individuals were in fact achromats, exhibiting the normal composite spectral responses but failing to perceive the chromatic information

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associated with the P– and Q–channels of vision.

15.4.6.1.4 Aphakia

Although obviously abnormal, humans who have had the lens of their eye removed are known to respond to ultraviolet light at wavelengths considerably shorter than the short wavelength skirt of the Rhodonine9 chromophore. Some aphakic patients have been found to respond to irradiation in the 310-360 nm. region19, the very same region to which many UV sensitive animals respond. It is reasonable to assume that these humans are exhibiting the presence of a fourth chromatic channel in human color vision associated with the chromophore Rhodonine11 with half amplitude parameters of 0.300 and 0.385 nm. It is even reasonable to assume that this chromophore is found in many, if not all, human retina.

The aphakic reports seeing “blue” and not “purple” in the 0.300 to 0.385 nm. spectral region. This report is worthy of further study; is the subject sensing a separate ultraviolet hue but calling it blue because he doesn’t know a different name for it, or is he sensing a separate ultraviolet hue but perceiving it as blue. It would be interesting to know whether the subject can be trained to separate the blue and ultraviolet spectral regions in his perception.

15.4.6.2 Representation of abnormalities related to color FIG MISSING

Figure 15.4.6-1 (Fig xxx+2) explores this chromaticity diagram more fully with regard to abnormal color vision in humans. If the axes of this diagram are defined in terms of the sensations registered at the higher cognitive centers, then it is possible to extend the diagrams to also include auxiliary axes corresponding to the outputs of the lateral cells generating the initial difference signals. In the case of the subject with normal color vision, the gain characteristic lines will always be at 45 degrees on this presentation. If a gain line decreases in slope as indicated, the subjects sensitivity to color differences related to that axis will be reduced until he reaches either the deuteranopic state (can not differentiate orange-red from yellow-green) or the pentanopic state (can not differentiate blue-violet from yellow-green). If both of the gain lines of the subject are reduced to zero, he is defined as an achromat. Under any of these conditions, the subject will still exhibit a normal photopic luminosity function since this characteristic is independent of the chrominance channels.

15.4.6.3 Abnormalities of luminance, orientation, or form OUT OF SCOPE

These abnormalities are beyond the scope of this work. Many of them lead to a feeling of unease. Vertigo is a major category within this spectrum of unease.

15.4.6.4 Abnormalities related to stereopsis OUT OF SCOPE

[xxx see section 18.8.2.3 ]

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Glycogen $\rightarrow$ pyruvate (aerobic conditions)
Glycogen $\rightarrow$ lactate (anaerobic conditions)
pyruvate $\rightarrow$ a-ketoglutarate (TCA)
a-ketoglutarate $\rightarrow$ glutamate (glutamate shunt)
glutamate $\rightarrow$ GABA + CO$_2$ (electrostenolysis)
GABA $\rightarrow$ glutamate (transamination)
GABA removal by diffusion (alternate)
GABA removal by transamination to succinic semialdehyde

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