Excerpts from

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.

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Vision Concepts
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[xxx consolidate Tootell appearances]
[xxx group computational anatomy with the examples in the 30 Jan 2015 message to Bruno Galmar in Section 15.5.2.3]

15 Higher Level Perception
PART II
Signal (abstract) Extraction and Interpretation [1]

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. 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*. This description is sufficiently advanced, compared with 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." The focus of Part II is on the extraction of abstract signals from the visuotopic signals presented to the feature extraction engines, and the ultimate processing of those signals.

15.5 Recent changes in the visual system baseline, ca 2002

[xxx review Shepherd, 1998, 4th edition before releasing a new version. Some material referenced in Part I]
A plethora of new information has recently become available on the role of the old brain, the *paleo*-cortex, in vision. The *paleo*-cortex will be defined as all of the brain other than the *neo*-cortex (the two cerebral hemispheres) and the spinal cord. Understanding this material has been greatly enhanced by three recent changes in the research environment. First, the arrival of computer-aided 3-dimensional reconstructions of individual elements and areas of the paleo-cortex allow a much more precise level of discussion. Second, the arrival of advanced non-invasive imaging techniques has provided the first dynamic information on the operation of the cortex (including signaling) related to vision. Third, nuclear chemistry has allowed the tracking of certain chemicals through the complicated steps involved in powering the neural network.

The work accomplished during the last decade of the 20th Century has had a profound impact on our knowledge of how the neural system works. This is true with respect to both the peripheral and central neural systems. While data collected prior to this decade continues to be of utility, the reader is cautioned to question any hypotheses, proposals, models or claims concerning the neural system presented prior to 1990. They are probably archaic. This even extends to the common wisdom that the primary visual cortex plays a primary role in vision. There is ample clinical evidence that the primary visual cortex is not necessary for meaningful and useful human vision (See **Chapter 18**). The occurrence of Blind Sight, sight in the absence of a functioning striate cortex, is now well documented. Peters & Rockland have edited the current (1994) bible concerning the primate visual cortex. They put it this way, "Inactivation studies, as described by Bullier, et. al., raise some queries, supported by anatomical results, as to the paramount importance of area 17 as a funnel for visual processes."[2] Additional material on this subject appears in Chapter 8 of their work. While the title of their volume 10 has some syntactical complexity, these authors generally use the term "primate visual cortex" rather than "primary visual cortex" because of this situation.

Understanding can also be enhanced by clarifying a variety of concepts employed previously, particularly with respect to visuotopic mapping, the projection of object space onto the topographically oriented circuits of various elements of the brain. These concepts will be discussed briefly in the following paragraphs of this section and will then be developed in detail and applied in **Section 15.6**. The new material has also caused a rewriting of **Section**

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[1]Released: April 30, 2017
[2]Peters, A. & Rockland, K. (1994) Cerebral Cortex, vol. 10, Primary Visual Cortex in Primates. NY: Plenum, pp ix

1.2.3 on the phylogeny of vision. This material highlights the fact that a selection of primates can no longer be used in research related to the maximum performance of the human visual system. The system contains components and circuits that are either rudimentary or absent in these lower species. With an understanding of these new elements and mechanisms, a new **Chapter 19** on the Mechanisms and Capabilities of Reading has been introduce to the work.

This Chapter will discuss higher level (both *paleo*-cortical, and *neo*-cortical) signal processing. Of greater 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 but not well modeled. Before 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[3]. 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 optimum skeletal-motor operations associated with vision. However, the system can perform at a greatly reduced level following its destruction.

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[4] reflects his paradigm shift in thinking as do his articles after 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 after 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[5]. In those, he notes the absence of an intersection between the vertical and horizontal meridians in V1. He also notes 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 equivalent waveform parameters in temporal space. These temporal waveforms must eventually be converted to a vector representation 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).

Tootell & Hadjikhani, along with a group of brain researchers largely unknown to the vision literature, have recently provided additional data of great significance to understanding vision. Tootell & Hadjikhani even question the existence of V4 as it is conventionally described and normally represented[6].

Most of the vision textbooks of the 1990's and 2000 have not incorporated Zeki's *new* views nor the work of Tootell and other brain researchers. This is unfortunate. Their work is being confirmed daily using the newer techniques of nuclear imaging and magnetic interference.

The conceptual "pretectum" used previously in this work is defined more precisely in this PART. It consists of the

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[3]Spillmann, L. & Werner, J. (1990) Visual perception: the neurophysiological foundations. NY: Academic Press. **[My Library]**

[4]Zeki, S. (1993) A vision of the brain. London: Blackwell Scientific Publications

[5]Zeki, S. (1978) J. Physiol. (London), vol. 277: Three papers pp. 227 to 290

[6]Tootell, R. & Hadjikhani, N. (2001) Where is 'Dorsal V4' in human visual cortex? Retinotopic, topographic and functional evidence *Cerebral Cortex* vol 11, pp 298-311

perigeniculate nucleus and pulvinar couple in the following sections. This definition resolves a difference in terminology between those investigating the lower chordates and those studying the primates.

15.5.1 Preview of the revised top-level block diagram of the visual cortex

This major section will build on the previous discussion and introduce new material from a variety of recent sources. Since all of the material taken together leads to a substantially different understanding of the cortical portion of the visual system, **Figure 15.5.2-1** is offered as an aid to its understanding. While the figure is complex, it is also informative. The recent work related to the thalamic reticular nucleus of the diencephalon has provided, for the first time, a rationale for the existence of striated and reticulated neural tissue in that element. These areas of neural tissue are clearly reflecting the topology of the underlying neurons that lie parallel to the surface of the brain tissue. The three areas shown surrounded by a gray halo are all described using either the term striated or reticulated. The detailed topology of two of these areas appears nearly identical to the topology of man made multidimensional correlators made using microcircuit technology. These are the areas labeled the perigeniculate nucleus, PGN, and the striate cortex. Correlators of this type are usually used to determine the presence of specific patterns of signals and then pass that information to subsequent circuits. The detailed topology of the third area (labeled the control point) appears nearly identical to the crossbar switching technology used in the telephone and data switching industries. This area is also described as the switching part of the thalamic reticular nucleus, TRN. The area labeled superior colliculus and cerebellum is shown with one-half of a gray halo. This area will be discussed in greater detail in **Section 15.6.5**.

The lateral geniculate nucleus, LGN, is shown without a halo in the above figure for a specific reason. It does not exhibit the distinctive striated or reticulated surface, and it appears it performs a different function. The LGN appears to perform a more localized comparison, rather than correlation, function. This function is designed to extract stereo-optic signals leading to proper vergence and then to combine the signals from the two eyes into a composite set of R-, P- & Q- signals for delivery to the occipital lobe of the brain.

Both multidimensional correlators, the PGN and the striated cortex appear to produce complex output signals on a number of parallel neural paths. These signals must be passed to orthodromic circuits for further analysis. These circuits are typically lookup tables. In the PGN, the associated lookup table appears to be located in the nearby

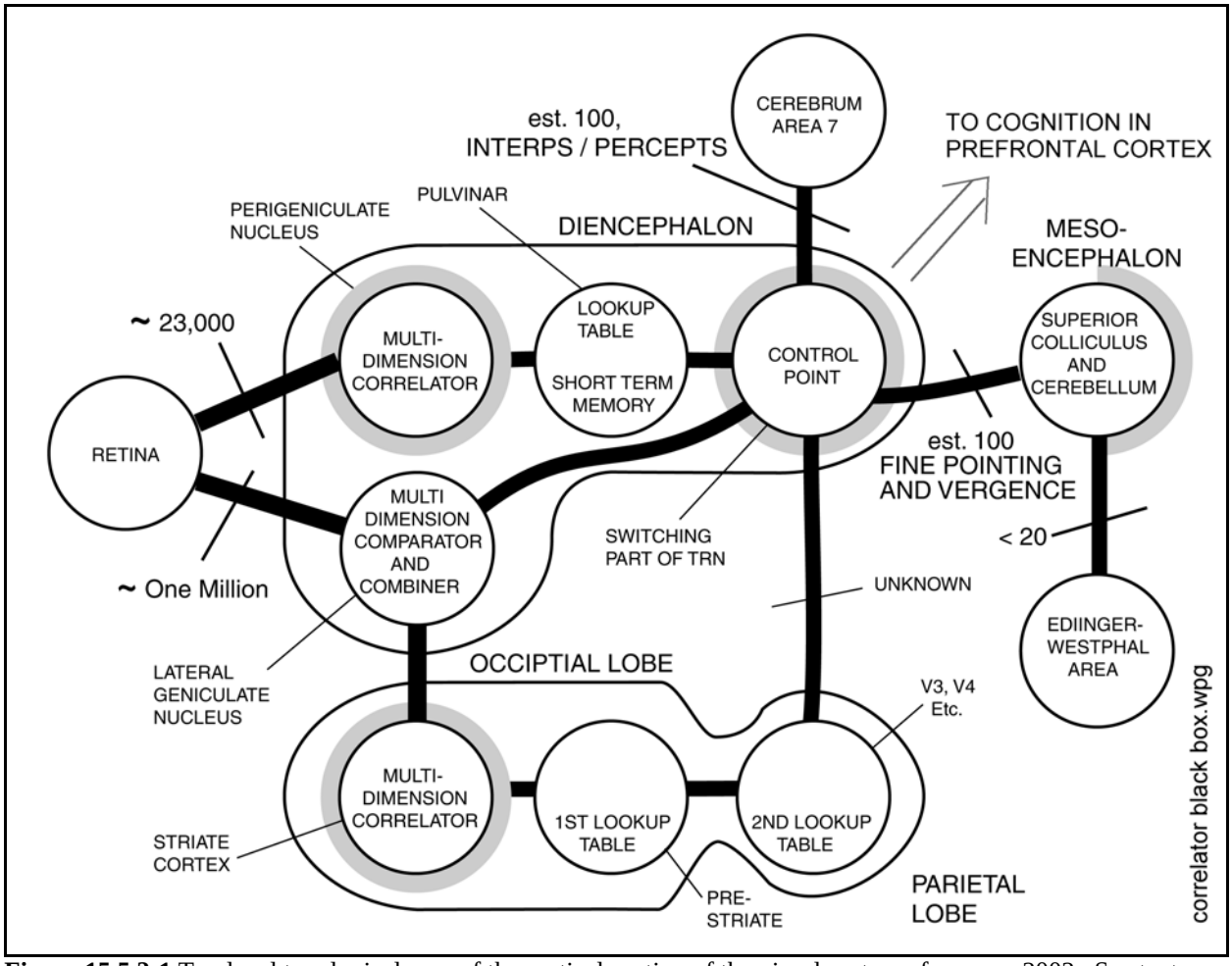

Figure 15.5.2-1 Top level topological map of the cortical portion of the visual system of man, ca 2002. See text.

pulvinar. In the case of the striate cortex, V1, the lookup table appears to be located in the nearby prestriate area, V2, of the occipital lobe of the brain. It may extend into the areas known as V3 and V4 of the parietal lobe. There is a question of whether these lookup tables operate in parallel in order to achieve more capacity, or whether they work in series to provide a greater degree of data reduction. Although not shown in detail, a similar question concerns the pulvinar. It appears this body must contain at least a short term memory capability (possibly a simple shift register) allowing individual input signals to be assembled in series.

Because both the PGN and the striate cortex appear to operate in close cooperation with adjacent elements, the pairings will be labeled the PGN/pulvinar couple and the striate/prestriate couple later in this section. The last label is not completely satisfactory since it is meant to include areas' V3 and V4. An alternate label might be the striate/V_n couple where $n \geq 2$ denotes the sum of all areas other than V1.

In both the PGN/pulvinar and the striate/$V_{\geq 2}$ couples, it appears the supporting circuits operate in serial because the signals at these orthodromic locations become less and less visuotopic with distance from the retina. They become essentially abstract (sometimes described as diffuse).

Numbers are shown next to several commissure in the figure. They show the known or estimated number of individual neurons in each commissure. The number leading to and from the striate/$V_{\geq 2}$ couple is not currently known. However, recent research has shown that the number of neural paths leading to this couple is similar to the number returning to the diencephalon.

The control point is shown accepting abstract signals from both the PGN/pulvinar and the striate/$V_{\geq 2}$ couples and passing them along to both area 7 of the parietal lobe and to the superior colliculus. These functions will be addressed further below. However, it should be noted that the control point accepts signals from all sensory modalities and aids in the creation of the saliency map probably located in, or near, area 7. It also directs signals to the cognitive (stage 5) circuits of the prefrontal cortex.

Each area shown in this figure will be discussed in detail below.

15.5.2 Computational ability of the brain and neural system

Additional visibility has appeared concerning the computational tools used in the visual system. The tools used reduce the computational workload within the system significantly.

15.5.2.1 Transcendental calculations have not been observed in the brain

Continuing the previous position, no new evidence has emerged suggesting calculations involving transcendental functions (sines and cosines, etc.) are performed within the brain. An old paper by Graham appears to remain relevant to this assertion[7]. To the contrary, massive and substantial evidence has appeared showing the brain uses one and two-dimensional string matching techniques and lookup tables to avoid the need for such calculations. Lookup tables allow the routine, and rapid, use of information previously programmed via the learning process (discussed in **Section 15.4**).

Robinson, and many other investigators, have described the direction of saccades in response to certain stimulations using polar coordinates. While such coordinates are convenient for discussion purposes, remembering that the underlying computations are not performed in polar coordinates is important. Therefore, it is likely that the saccades reported by Robinson were either due to the stimulation of neurons within a lookup table, or neurons leading to a lookup table within the superior colliculus or cerebellum.

The fundamental topologies of the correlators and lookup tables found in the neural system are remarkably similar to the topologies found in man-made microcircuits. They are in-fact serving the same functions. An examination of the PROMs, EPROMs, RAMs and PLAs of electronics will aid greatly in understanding the operation of the visual system.

In later discussions, a combination of a correlator element and a memory element (lookup table) working as a group will be advantageous. Such a group will be described as a couple, such as the superior colliculus/cerebellum couple (SC/cerebellum couple).

15.5.2.2 Fourier transform calculations have NOT been observed in the brain

Many authors have speculated on the use of the Fourier Transform (and occasionally the La Place Transform) in conjunction with the visual process. In general, these discussions are highly conceptual and do not address the neural circuitry required to implement a Fourier Transform. This work has not uncovered any evidence that the neural system is able to carry out the mathematical steps required in a conventional Fourier Transform, the La Place Transform or even a convolution integral.

Similarly, various authors have suggested that the visual system employs Fourier filter techniques to analyze simple patterns presented in object space. Some have made an analogy between the aural and visual sensory systems, on the assumption that the aural system uses some form of Fourier Analysis[8]. This is not a rational comparison. There is no data supporting the ability of the neural system to compute a Fourier Integral whether in a one dimensional or two-dimensional space.

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[7]Graham, N. (1981) The visual system does a crude Fourier analysis of patterns *In* S. Grossberg, *ed*. Mathematical Psychology and Psychophysiology, SIAM-AMS Proceedings, Volume 13, pp. 1-16. Providence, Rhode Island, American Mathematical Society
http://www.columbia.edu/~nvg1/normster_pdfs/1981GrahamFourier.pdf

[8]Xxx, xxx. (1985) xxx *In* Peters, A. & Jones, E. ed, Cerebral Cortex, vol. 3, Visual Cortex. NY: Plenum, pp 405-407

The circuitry found within the neural system strongly suggests that the system is based on lookup tables formed in write-once, then read-only memory and created originally via a learning process. An exception is a limited amount of genetically defined preprogrammed read-only memory. These lookup tables can be arranged to support any number of degrees of freedom, e. g., time, spatial dimensions, spatial orientation, chirality, color, brightness, correlation with other sensory modalities, etc.

While the use of Fourier and La Place techniques are very useful intellectual tools developed by man, no use of, or need for, such tools within the functional circuits of the neural system have been documented.

15.5.2.3 Correlators & Lookup tables are key mechanisms

Figure 15.5.2-2 illustrates the general concept of the correlators and lookup tables used in the individual bodies of the thalamus, including the PGN, LGN and TRN. The concept is also employed in the striate cortex. Recall first that, the visual system is a change detector. All of the neurons associated with vision within the CNS operate with respect to changes as a function of time. Until the correlation processes, which are the subject of this section, these changes have been with respect to time in a unitary temporal signal. The resulting signals are most easily described in terms of a very efficient NRZ (non-return-to-zero) code. The above engines, supported by others, have two primary tasks. First, the task of sensing the changes received via individual temporal channels in the context of a spatial array (of arbitrary extent). Second, the task of providing a "machine language" output that can be used by either the POS or the cerebrum. By accepting the fact that the main correlation (and/or translation) process relies upon the detection of changes, the figure can be simplified.

By weaving sensing lines through a multidimensional (only two shown) array of signaling lines, it is possible to detect a specific pattern within the nodes shown. These nodes are excited by the presence of a signal on each of its input lines (one from each dimension). This forms the basic mechanism of any programmed read-only-memory, PROM (also known as a programmed logic array, PLA). Here, the sensing lines will provide an output only if they do not intersect with any excited nodes. Think of this as finding a white line of a specific length at a specific place on a piece of black paper. Two sensing lines have encountered this criterion. The output signals are in machine language and represent symbolically the presence of the above white lines.

From the output of a PROM onward, the signaling channels are no longer arranged retinotopically. The symbolic information contained in the signals may still carry a retinotopic label. In the case shown, if the two output lines were combined in a subsequent circuit, they could represent symbolically an image consisting of two diagonal lines of specific spacing.

Notice that the source of the two sets of input signals to the processor was not discussed. These can represent any signal information. For the LGN and the PGN (part of the TRN), the signals are retinotopic and the array can be considered a spatial correlator. For area 17, the inputs can be considered partially retinotopic (or crudely retinotopic). However, subsequent similar processors receive machine language inputs and produce machine language outputs. This is the typical situation in the pulvinar, many other engines of the thalamus and in areas 18-22 of the occipital lobe. It is the norm in the engines of the P-O-T and frontal lobes of the CNS.

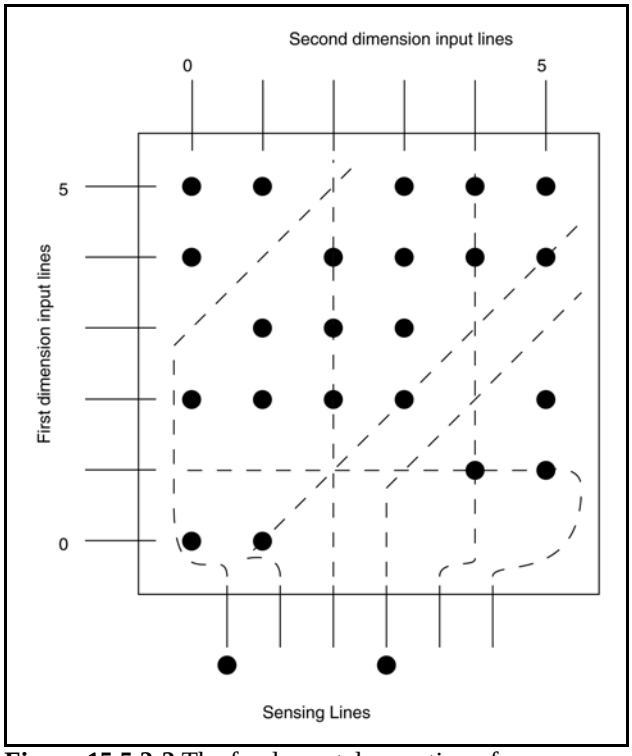

Figure 15.5.2-2 The fundamental operation of a programmed read-only memory. Signal inputs related to either dimension typically excite every node along their line of the array. However, a node is only turned on when it receives excitation along both axes. Even under the condition shown, where over 80% of the nodes may be excited, a machine language output appears on only two of the sensing lines (in this case, only where no pairs of signals were sensed at multiple locations during one sensing cycle).

Finally, we come to the processors used to generate

and perfect oculomotor, skeletal-motor and other efferent neural signals. Here, the processors are wired to operate in reverse. They can receive simple input instructions and generate a suite of individual output instructions that can be distributed to specific motor signal generation nodes. These signals can carry intensity information and also any delay programmed into the specific vector.

The above conceptual processors can be implemented in a variety of ways within the neural system. In the above processors, the sense lines are easily formed by neurites of extended length and relatively small diameters. The signal lines correspond to axons and their laterals. There may or may not be Activa located within a discrete neuron placed at intersections of signal lines. Man typically prints straight signal lines, sometimes in a chevron fashion, with interconnections close to the axis of the line. However, there is no requirement that the lines be straight, or even collateral free. The figures of the axons shown in Chapter 3 of Sherman & Guillery are good examples of the biological equivalent signal lines. Some of them are several hundred microns long with short collateral spaced evenly along the axon. These collaterals end in synapses that were not functionally defined by those authors. It is proposed that these synapses are at nodes. These nodes may contain a small compact neuron acting as a short term storage element, or they may consist of only a section of a neurite accepting inputs from multiple axons. When connected, these sections of neurite would form one of the sensing elements of the complete array. Note that with the availability of collaterals, there is no requirement that the two sets of signal lines be orthogonal to each other. They may all enter from one side, or from a variety of directions. This is especially true in multidimensional arrays.

The use of multiple correlators in parallel explain the high signal processing rates of the CNS. With an average neuron exhibiting 2500 synapses with which to interconnect with other neurons, a few thousand neurons can form a large number of individual correlators. These neurons can quickly compare an input pattern with a multitude of stored patterns and issue one or more signals describing the correlations found within tens of milliseconds.

15.5.2.4 Computational anatomy

Besides the computations performed within the feature extraction engines of the visual system, the spatial arrangements, and rearrangement of various groups of neurons within commissure are of great importance in vision. Most readers are familiar with the contralateral and ipsilateral arrangement of the signals from the two retinas performed by the optic nerve, optic chiasm, etc. The mappings presented to the lateral geniculate nuclei of the paleo-cortex, and to the lesser known perigeniculate nuclei reduce the computational effort required of the feature extraction engines immensely. This process of rearranging the flow of neural signals in a spatial context (not necessarily related to the input stimulus) is of great value in the visual system. The term computational anatomy was introduced by Schwartz in 1980 to account for this significant phenomenon. It occurs in both the temporal domain, by varying the length of the commissure, as well as in the spatial domain. One example of each is given heere.

1. The path lengths of the individual neurons from the photoreceptors of the retina to the optical nerve vary significantly in length. The result is that the great many signals delivered to the CNS are not synchronous. This is not a serious problem in the diencephalon. However, it is for the visual cortex of Brodmann area 17. To compensate, the neurons traveling from the diencephalon to area 17 are spread out in what is called Meyer's loop. The effect is to introduce compensatory delays without the use of separate delays lines or shift registers. This is an example of anatomical computation.

2. Tootel et al. have demonstrated that the visuotopic image recorded by the retina is transformed into a totally different image on the surface of the visual cortex of Brodmann area 17 (**Section 15.6.5.3.5**). The effect is startling and very consequential! Straight lines are converted into ellipses. Circles in the visual field are converted into straight lines on the cortex. Thus a circle can be identified by a summing neuron that collects the signal current from all of the neurons associated with a specific straight line in area 17. No complicated calculations are needed. This is an example of anatomical computation.

The term computational anatomy has arisen in the field of large scale computer assisted computation related to image analysis and stage 4 information extraction. Most of the material in that field may have great utility in the mimicking of human information extraction but little of it represents an actual modeling of neural circuits (See **Section 19.10.5**). Many of these papers do not distinguish between stage 4, information extraction, and stage 5 cognition. See also the paper in Whneuron/ computational comp paper/The Neural Architecture and Operating Modes related to attention, and image information extraction and search for RBM xxx This work has not developed a clear delineation between these stages and currently has lumped the discussion of Boltzmann Machines of various types in **Section 19.10.5** of “Processes in Biological Vision.”

15.5.2.4.1 Use of the term retinotopic should be avoided

Many investigators have used the term retinotopic to describe the geometry of a spatial map occurring within the

neural system in terms of an image in object space that they projected onto the retina. They made the assumption that the computational anatomy (the physiological optics) of the ocular creates a linear representation of object space on the retina. This is not true for the off-axis situation because of Snell's Law. The representation is compressed radially as a function of the reciprocal of the sine (the cosecant) of the angle from the line of fixation. It is also not true in the birds of prey, due to the field lens formed by the neural tissue of the retina. The representation is expanded in the foveola, compared with surrounding areas. Therefore, the term visuotopic should be used in the research environment when the reference scene is in fact in object space.

Davenport has introduced another complication in defining maps[9]. In tracing the neural paths from the retina of chicks to their tectum, he has used the term retinotectal map. He describes this as "coordinate maps of retinal ganglion cell bodies across the retinae and their terminations across the tecta." This definition highlights the need to differentiate between a map of ganglion cells versus the map of photoreceptor cells of the retina. It also highlights the difference between the ganglion cell maps related to luminance signals and those related to chrominance (and/or polarization) signals.

15.5.2.4.2 Hypercomplexity as the antonym for visuotopicity

Investigators have struggled with how to describe neural circuits that exhibit less and less correlation with the spatial geometry of the original image in object space. Hubel and Wiesel introduced the concept of hypercomplexity, when studying the cat, to describe the degree of complexity they were encountering. Although the term has not become common, it appears to offer a descriptive antonym to the term visuotpicity or retinotopicity. As the visuotopicity decreases, the hypercomplexity (or level of abstractness) increases.

15.5.2.5 Description of individual signal paths and commissure

Sherman & Guillery have recently described the signal paths and commissure associated with the visual system in terms of first order (FO) signals and higher order (HO) signals. In the process, they note that they have not included neural paths carrying analog signals because they are difficult to investigate using current techniques. Their discussion is limited to projection neurons exhibiting action potentials. Their discussion is also constrained to using the LGN of the cat as a model. They have defined first order signals and paths as those involving signals that have not yet been processed within a cortical portion of the visual system. All signals that have been processed, at least initially, are labeled higher order. This nomenclature will not be adequate for the purposes of the following discussions. The reasons will become apparent in later discussions. A broader framework will be used here. It includes a variety of signals described primarily by their signal content and degree of abstraction. These signals may have originated in more than one sensory modality and may be combined into quite complex signals representing the environment surrounding the subject. This complex signal format is associated with a saliency map. The putative saliency map is the primary resource used by the higher level cognitive centers to understand their surroundings. Among the HO signals of the visual system are alarm signals extracted from various FO signal modalities, and supervisory signals extracted from various abstract signals. The latter include the servomechanism signals used to manipulate the line of fixation of vision. Similarly, the cognitive centers may initiate both supervisory and command signals fitting within the context of HO signals.

As expected in the more complex mix of FO and HO signals, exhibiting various levels of abstraction, the comment by Sherman & Guillery, that maps related to HO signals are very elusive, is an understatement. Their paper will be discussed in detail below.

15.5.2.5 Description of individual signals and methods of neural coding

The following analyses will begin to discuss specific signal profiles and coding schemes used in vision. Two books have provided valuable contributions in these areas. Tasker, et. al. have provided a large volume of experimental work, most of it under stereotaxic conditions[10]. They provide statistical data on the variability of given neural sites among humans and discuss various efforts to deduce the "machine language" codes used in the different sensory and command signal paths. It can be said that they did not discover, or decode, any of the codes used in the neural system: In 1982, they said "We lack the program with which to communicate electrically with the greatest computer of all." They did observe a range of responses after shocking the system, sometimes with signals patterned after

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[9]Davenport, R. Thies, E. & Nelson, P.. (1996) Cellular localization of guidance components in the establishment of retinotectal topography, *J Neuroscience*, 16(6): 2074-2085.

[10]Tasker, R. Organ, L. & Hawrylyshyn, P. (1982) The thalamus and midbrain of man. Springfield, Il: C. Thomas, Publisher pp 81-84 & 204-212

previously recorded patterns. Their results support a position developed below, that many neural signals are sent in parallel word form over multiple neural fibers.

Steriade, et. al. have provided a wealth of recorded waveforms, primarily involving neural paths to, within and from the thalamus[11]. The most important discussion shows that some action potentials are generated within the thalamus at clock rates as high as 800-1000 Hz. They also recognize the oscillatory nature of the action potential generating neurons and present a state diagram based on an autocatalytic reaction. This diagram can be used more effectively to explain the electrolytic mechanism of this work. Many of their waveforms show distinct threshold levels. A few waveforms exhibit a change in slope near the peak of the action potential when displayed on an expanded time scale. However, most of their waveforms were recorded with a circuit exhibiting excessive high frequency response. The result is large amounts of overshoot and distortion in the actual waveforms. It is not clear whether the high frequency pre-emphasis was intentional or due to inadequate probe compensation.

Steriade & Glenn provide a more detailed report on the high frequency action potentials of the thalamus. They also describe the variability in the propagation velocity of the signals over different axonal structures[12]. The parameters provided broaden the range of action potential characteristics discussed earlier in this work. They also appear at locations consistent with the architectural requirements suggested by this work.

15.5.2.5.1 Use of rhythmic and burst to describe action potential streams

The literature of Brain Research has recently adopted the terms rhythmic and burst (sometimes tonic and burst) to describe action potential streams. Sometimes, the terms have been used to define different electrophysiological types of neurons. In fact, these descriptors are related to the type of stimulus applied to the neuron and not its innate character. As an example, merely changing the average level of the stimulus used will cause the action potential stream to change form as shown in the visual responses of Figure 9 in Sherman & Guillery (1996). They chose to inject current into the neuron under test, instead of changing the retinal stimulus, and by that cause an equivalent change in bias. The results in their Figure 7 are a bit more complex because of the time constants of the neuron they chose to study (possibly in combination with their test set). The changes in the shape of the analog portions of those waveforms suggest an uncontrolled change in a time constant. It was probably due to the power source used to change the DC potential. This would change the instantaneous voltage signal applied compared with the threshold portion of the circuit although the applied current remained constant as shown. These matters are discussed in detail in **Chapter 9 & Chapter 10 PART II**.

Using the term tonic to describe a series of equally spaced phasic signals can cause confusion when examining chrominance and polarization sensitive channels. These channels exhibit a continuous stream of action potentials where the precise spacing between them is due to the input stimulus. Lacking a stimulus, the spacing returns to a nominal value. The nature of the pulse stream in the luminous channels can be much more complex because of the various effective time constants present because of adaptation.

15.5.3 Specific maps within the visual system

Researchers have reported on several “maps” associated with different morphological structures within the visual system. The maps are fundamentally topological but the neurons forming the networks sometimes affect the surface topography of the overall structure. The more complex ones require an excellent understanding of the underlying mechanisms and processes to interpret.

Many of the reported maps are based on a very limited number of electrophysiological probes. As a result, the maps are more conceptual than definitive.

15.5.3.1 Framework for discussing maps

The literature contains a conflicting set of comments and terminology concerning the maps related to vision found in the neural system. They generally do not recognize the closed loop nature of virtually every neural path (an action results in a reaction, even if subtle). A more fundamental framework can be developed based on **Sections 11.1.4** and **15.2.3 xxx** of this work. **Section 11.1.4** develops the basic signaling path within the neural system as consisting of an arc. This arc involves an afferent sensory path rising to a node and an efferent action path descending from that node. These arcs can be assembled into a hierarchy by replacing (or bridging) the node with a higher order arc. The elements of the higher order arc may or may not replace the original function of the first arc. This function may

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[11]Steriade, M. Jones, E. & Llinas, R. (1990) Thalamic oscillations and signaling. NY: John Wiley

[12]Steriade, M. & Glenn, L. (1982) Neocortical and caudate projections of intralaminar thalamic neurons and their synaptic excitation from midbrain reticular core. *J. Neurophysiol*. vol. 48, no. 2, pp 352-371

involve computation designed to extract information from the basic signals conveyed over the afferent signal path. If it does, the signals within the node, and higher level nodes, can be considered higher order, HO, signals in the language of Sherman & Guillery. However, if the signals passed up to the higher node remain in their basic form, Sherman & Guillery would label them first order, FO, signals. Those authors did not address the descending signal paths. Following their logic, the last stage of the efferent signals might be labeled last order, LO, signals. These LO signals can be mapped to the particular responses of specific (and individual) muscles.

Section 15.2.3 shows that there is a wide range of interconnecting paths within the visual nervous system. Within the cortex, these form a hierarchy of arcs (and other interconnections) that need a more general terminology that calls for more definition within the label "higher order." Most of the important paths within this structure are defined in **Table 15.2.3-2**. The signals moving along these paths exhibit a variable degree of spatial relationship with object space. They become more abstract with distance from either the afferent or efferent terminus of the first order arc.

The degree of abstractness can vary between the outputs of a given node. In the classic case, the **awareness mode** outputs of the LGN's proceeding to the striate cortex remain highly visuotopic, leading to the overly broad definition of the *paleo*-cortex as primarily a relay of information. However, the **alarm mode** and **stereo mode** outputs of the same LGN's exhibit virtually no visuotopic characteristics. They are encoded in a machine language designed to control the vergence and saccades functions. These fundamental differences require recognition. A similar situation arises in the afferent signals of vision. While muscular (and adrenal system) responses may be mapped, they can also be traced back to abstract signals within the nodes of the neural system. Overall, the muscular and adrenal system responses cannot be mapped visuotopically to the retina or object space. They clearly cannot be mapped visuotopically on a one-to-one basis **or** with high precision. As an example, a clearly abstract **volition mode** command can cause the eyes to change their line of fixation without any stimulation of the retina. On the other hand, it has been shown that **alarm mode** signals can cause an involuntary response by the precision optical system to change the line of fixation. The individual only becomes aware of the response later. This work will show that labeling the diencephalon of the paleo-cortex a relay is grossly inappropriate.

When discussing maps within the visual system, it is necessary to recognize that the levels of development of these maps, their complexity and sophistication, are strongly related to the phylogeny involved. It will be shown in this section that there are two grossly different types of neural maps and they exist in at least two different contexts. Some are found in the afferent signal path context. Others are found in the efferent signal path context. There are also neural maps within the frontal, temporal and anterior portion of the parietal lobes that are too abstract to interpret at this time. These are the abstract maps currently being documented, at a gross level, in MRI and PET laboratories. The orthodromic projections associated with the afferent paths and related to object space are generally described as visuotopic or retinotopic maps. There are also the antidromic *projections* along the afferent paths. Antidromic afferent channel maps, also called receptive field maps (see **Figure 15.1.2-2**), have not been produced in great abundance because of the difficulty in interpreting them. This difficulty is compounded by the lack of a framework in which to compare them. There are also orthodromic and antidromic *projections* related to the efferent paths. The antidromic projections are not signal paths. They are man-made aids to understanding the operation of the system.

Figure 15.5.3-1 provides an extension of the neural hierarchy developed in **Section 11.1.4**. It uses the ladder approach up to the point of the saliency map. In this approach, one rail corresponds to the afferent signal paths and the other rail the efferent signal paths. Only signal paths are shown. The figure can be compared to a simpler version by Fuster[13] It can also be compared to the caricature by Edelman in Fuster[14]. This caricature shows the approximate role of Wernicke's area and Broca's area in the production of speech based on hearing. Unfortunately, all of the signal paths are shown as bidirectional in this figure. [**Figure 15.5.3-1**] begins with the environment exterior to the subject. While the visual portion of that environment is associated with the visual system, the same environment is sensed by the other sensory systems. The auditory sensory system shown on the left represents these other systems (touch, taste and olfaction) as well. Similarly, the skeletomotor system is shown on the right.

The somatosensory and skeletomotor systems incorporate many reflex loops between the afferent and efferent paths at a series of nodes, as suggested in **Figure 11.1.4-2**. The visual system takes a different approach. The visual system reorients most of these nodes into signal processing centers. Those within the retina create the multiple

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[13]Fuster, J. (1980) The Prefrontal cortex : anatomy, physiology, and neuropsychology of the frontal lobe. NY: Raven Press figure xxx Also in later additions.

[14]Edelman, xxx (1989) *in* Fuster, J. (1995) Memory in the Cerebral Cortex. Cambridge, MA: MIT Press, pgp 279-281

signals associated with the luminance, chrominance and geometric channels discussed earlier. An exception is found within the connections between the thalamus and the superior colliculus. These connections (particularly the alarm mode) could be considered a reflex path. However, most of them are more complex than in a typical reflex mechanism. They involve considerable signal processing in order to implement the precision optical system servoloop. They are also under the overall control of the thalamic reticular nucleus (TRN, not shown). The TRN can override many signals that would be considered reflexive otherwise.

All of the sensory and motor systems interact strongly at the thalamus/superior colliculus level. These interactions are frequently associated with the philosophers "zombie." The subject can interpret and perceive his environment and react to it. However, the reaction is largely reflexive. These reflexive responses may be either inate or acquired through previous experience. However, they do not involve cognition within the higher cortical centers.

The figure provides a clear distinction between visuotopic and abstract signal levels. Within the afferent signal structure, the goal is to extract the information from the signals and incorporated it in the saliency map that can be accessed by the higher cognitive centers and other elements of the parietal lobe. All of the awareness, analytical and instructions found within the saliency map (and an equivalent instruction register) are in totally abstract (symbolic or vectorized) form. The degree of visuotopic character in the signals decreases monotonically in passing through the PGN/pulvinar couple and the LGN/occipital couple.

A similar situation occurs within the efferent signal paths. For consistency, an instruction register has been shown at a level equivalent to the saliency map. The higher cognitive centers generate abstract instructions that are delivered to the superior colliculus over volition mode channels. The actual instructions may be so complex that they need to be decoded initially and passed to more structures than just the superior colliculus. These possibilities have not been addressed in detail. The unlabeled boxes are suggestive of this additional signal manipulation and may be associated with functional elements with labels like parietal premotor and motor areas. The superior colliculus has an interpretation duty essentially the opposite of the thalamus. It receives abstract instructions that it must convert into definitive commands for distribution to individual motor neuron control centers.

While the architecture of the sensory and motor systems can be considered hierarchal, the figure is drawn to highlight the fact that the architecture of the cognitive areas is not. Virtually all of the higher cognitive centers can access the saliency map and the instruction register directly. While it is possible a supervisory element exists among the higher cognitive centers (similar to the TRN within the interpretation and perceptual engines of the diencephalon), their association is collegial instead of hierarchal. The subject of a central supervisory element will be left to **Section 15.7**.

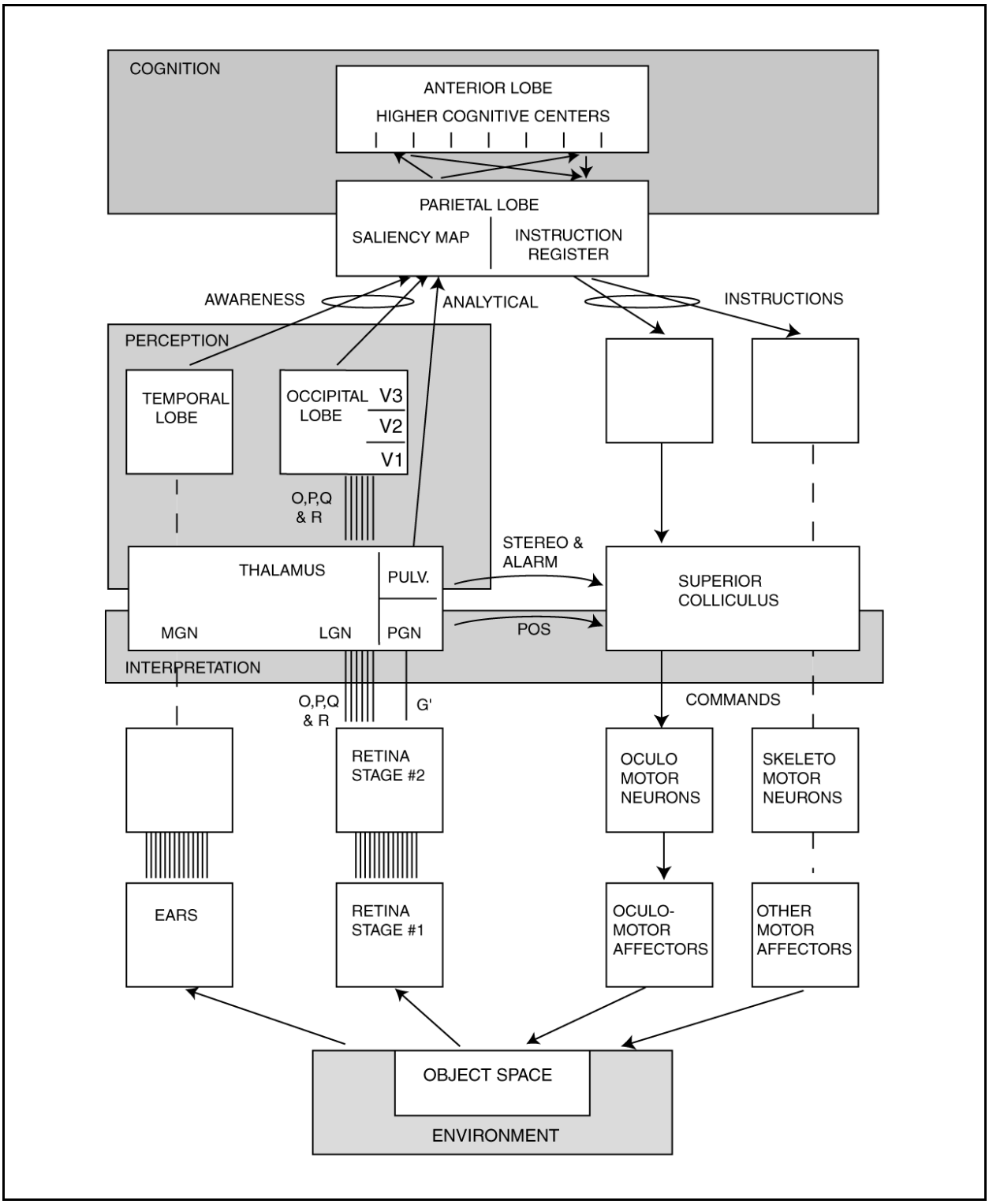

Figure 15.5.3-1 Signal flow within the neural system at the global level. Afferent signals proceed up the left side. Efferent signals proceed down the right. All signals above the perception level are in abstract (symbolic) form. Signals below the interpretation level are in visuotopic (environment oriented) form. The sensory interpretation and perception functions can be considered unisensory association areas. Above that level, all functions and messages can be considered multisensory, or multi-responsive, in character.

Figure 15.5.3-2 provides a framework for further discussion of visuotopic maps. The construction of this figure will be discussed in **Section 15.6.5.2.4**. xxx

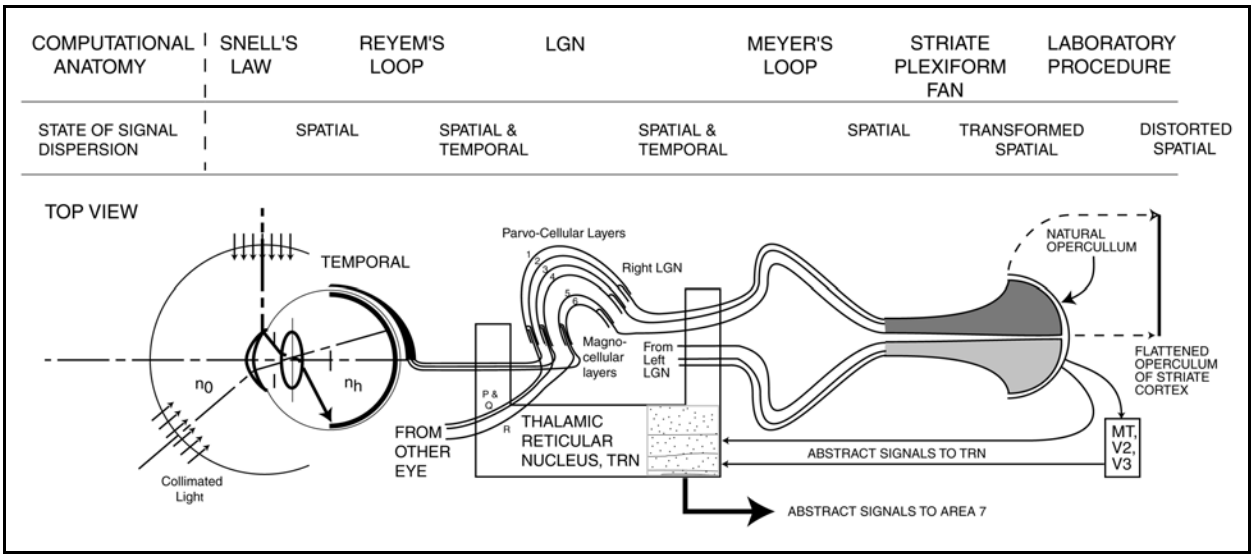

Figure 15.5.3-2 Steps in the creation of a visuotopic representation at the striate cortex. The key location of the TRN is shown. Signals pass from it through the LGN/Occipital loop and back to it. Snell's Law introduces a significant distortion between object space and the retinal map. The other major rearrangement of signals occurs in the commissure approacing the striate cortex. See text.

While the number of truly visuotopic maps is limited, the number of antidromic maps associated with the afferent signal paths is limitless, essentially equal to the number of identifiable feature extraction engines found in the brain. To definitize the number, it might be limited to those feature extraction engines outside the anterior lobe of the brain.

A mirror image situation arises when examining the efferent signal paths. There are both orthodromic and antidromic projections. The orthodromic projections are the most studied because some of them result in observable actions by the subject. However, the difficulty of exciting a single neuron must be appreciated, particularly if it is to be done *in-vivo*. The observed responses to a specific stimulus applied to a given group of nerves may be quite complex. This is true for two reasons. First the stimulus being applied is not in the machine language of the neural system. Second, if the stimulus is applied in the command generation area, it may propagate into the command implementation area and result in the transmission of many individual skeleto-motor commands. The only antidromic afferent paths studied to date at a detailed level involve staining and nuclear isotope techniques. These are frequently carried out in an *in-vivo* context followed by sacrifice of the subject.

15.5.3.2 Visuotopic mapping versus receptive fields

Historically, there has been a concerted effort to describe the topology of the signals within various elements of the visual system in terms of their geometric relationship to the scene projected onto the retina. While there is a clear visuotopic mapping of the scene onto many of these elements, the reader is encouraged to consider the goal of the system. The goal is not to replicate such maps ad infinitum. The goal is to extract information from the neural signals in an abstract form that can be used by the higher cognitive centers of the brain. The extraction process involves a great many feature extraction engines within the brain. These engines typically occupy a region of the brain with a diameter of 0.5-2.0 mm. Their thickness is frequently equal to the thickness of the cortical sheet, typically 0.5 mm. Depending on the size of the individual neurons, these engines typically include 125,000 to a few million neurons. This is the typical size of a man-made 486 microprocessor or RAM chips (see **Section 15.5.3**). There are several thousands of these engines, used both for feature extraction, cognition and command formulation. In total, the human brain contains many billions of individual neurons assembled from these engines. Only educated guesses (sometimes described as WAGs) are available concerning the actual number of neurons in the brain.

As recent authors have noted, there is a myriad of mappings within the visual system. However, confusion has appeared concerning the fidelity of these mappings. If one studies the reported mappings, it is seen that the fidelity of these mappings decreases with distance from the retina. This is true concerning granularity and spatial conformality and is to be expected. The confusion arises when one attempts to consider each map as a projection from object space. As one proceeds away from the retina, the receptive field, in object space, of each electrophysiologically probed location grows. In addition, adjacent neurons exhibit grossly overlapping receptive fields. Furthermore, as several authors have noted, multitudes of neurons in the pulvinar are stimulated when even the simplest images are projected onto the retina. These are the characteristics of signals associated with correlators and lookup tables. The individual neurons within these elements do not exhibit any spatial relationship with the input stimuli. They exhibit an abstract relationship (largely unknown at this time) with respect to the scene using a "machine language" (that is also largely unknown at this time). These relationships are determined within different feature extraction engines. The abstract output signals from these engines make up the signals transmitted on to the higher cognitive centers. Very little effort has been expended to date in attempting to decode the machine language used in vision.

Abstract signals of the type described above have previously been called "diffuse" in the literature. The term was chosen to reflect the receptive field associated with the neurons exhibiting these signals, rather than the content of the signals.

As will be shown below, many of the reported maps within lookup tables are not visuotopic. Those found in the pulvinar, in area 18 (also known as V2) and in the cerebellum are actually mappings of the receptive fields of the neurons (or engines) at those locations. They generally show no spatial relationship to the individual photoreceptors of the retina. Malach, et. al. have presented a recent paper focusing on the individual engines within area 18 (V2).[15] For the superior colliculus and cerebellum the neurons do show a broad spatial relationship to the motions of the oculomotor and skeletomotor in response to stimulation at that location. However, these associations are not based on direct, or first order, neural connections.

The features of relevant projection and receptive maps will be discussed in detail in the following sections.

15.5.3.2.1 Mapping as reported in the parietal cortex

Robinson, et. al. have provided a major and provocative paper on the nature of the responses of parietal neurons in the posterior of one of the area 7's of rhesus monkeys to simple object space stimuli. The stimuli were typically 3° x 3° and distinct from a smaller fixation point (typically 5 x 5 minutes of arc)[16]. The responses were shown earlier in [**Figure 15.1.2-1**] The receptive fields were very large, frequently one quarter or one half the full visual field. Many cells responded to both foveal and peripheral inputs. They noted; "There was in our sample, no indication of a retinotopic map more specific than a general preference for fields in the lower contralateral visual field." And, "Parietal cells were remarkable in their lack of visual specificity. We found no cells which had a requirement for stimulus orientation." These are the results expected by this work when measuring abstract signals previously extracted from retinotopic maps by the LGN/occipital or PGN/pulvinar couples.

Robinson, et. al. also provided latency measurements. Unfortunately, they used an extremely slow shutter with a rise time of four milliseconds. This caused them to use a bin width of 20 ms. As a result, their average delay before detection at the probe is between 80 and 100 ms. The range of latencies measured 47 to 214 ms. They also noted; "We have seen no off-responses in parietal neurons." This would also be expected for abstract signals. One of their conclusion was that data from the occipital lobe was unlikely to be projected directly to the area 7 of the parietal lobe because of their distinctly different signal characteristics.

They also note; "Area 7 receives rich projections from the limbic system; both the cingulate gyrus and the substantia innominata project to this area." Their conclusion 9 is, "We conclude that posterior parietal cortex is composed of neurons with sensory response, some of which associated information from the visual and somatosensory environment with internal data. This is a reasonable statement of neurons manipulating abstract data to and from the saliency map. Their discussion section begins with, "These experiments show that posterior parietal cortex should be viewed as a sensory association area. Cells here integrate visual and somatosensory information from the

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[15]Malach, R. Tootell, R. & Malonek, D. (1994) Relationship between orientation domains, cytochrome oxidase stripes, and intrinsic horizontal connections in squirrel monkey area V2. *Cerebral Cortex* vol. 4, pp 151-165

[16]Robinson, D. Goldberg, M. & Stanton, G. (1978) Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *J. Neurophysiol*. vol. 41, no. 4, pp 910-932

environment with behavioral data which are presumably generated internally."

The paper goes on to evaluate the relationship of this area to other somatosensory and motor signals. This leads to their definition of "saccade neurons, visual fixation neurons, tracking neurons, and hand projection neurons." All of these neurons are operating at an abstract level.

15.5.3.3 Orientation of visuotopic maps

Investigators have frequently attempted to understand the mechanisms of vision by understanding the orientation of the visuotopic maps found in the lateral geniculate nucleus and area 17 of the *neo*-cortex. The orientation is usually specified on a "global" basis with respect to the stereotaxic axes employed to define the brain of the subject. Efforts to define the orientation, through a field sign (or local sign) describing the relationship between object space and mapping space have encountered greater difficulty with distance from the retina. The problem has been particularly puzzling in the transition from V1 to V2, V2 to V3 and V3 to V4. The problem is centered on the fact that the areas with a higher numeric are ever more abstract and less and less visuotopic. Their global sign is determined by computational anatomy rather than the preconceived ideas of the investigator. As the investigators look more closely, they find the local sign, if recognizable, is controlled by the individual feature extraction engines. Some investigators have found large numbers of sub maps associated with areas V2 and higher. These are clearly receptive maps not projected maps. Their orientation, if any, is largely irrelevant.

The term local sign is of limited value when it varies significantly over small areas. Furthermore, the quantity being discussed is not a bipolar quantity, but the integral of a vector quantity. As shown below, each representation of object space can be described by a field map. Such maps are vectorial in character. The field vector at any point in the map defines the magnification factor (frequently called the cortical magnification factor, CMF) at that point. By resolving this vector into its meridional components, the magnification compared with the horizontal and vertical meridians and the angle of the vector relative to those meridians can be determined. Where needed, the term field value or field vector is more appropriate than local sign since the relevant quantity is a function that varies with position within the topological field being examined.

15.5.3.4 The maps associated with the afferent signal paths

Within the context of the above discussion, Sherman & Guillery provide the best available summary of the maps found within the thalamus[17]. As discussed in **Section 15.6.2**, additional segmentation of the thalamic reticular nucleus is needed before the material they present can be interpreted completely.

15.5.3.4.1 The major orthodromic maps of the afferent signal paths

The orthodromic maps are usually referred to as either visuotopic or retinotopic maps. The fidelity of the orthodromic maps degrades with distance from the retina as the information within the maps is extracted. The most familiar orthodromic maps are the pairs found in the LGN and the striate cortex. There is another pair in the PGN's. This pair is of higher spatial fidelity than either of the above pairs. It provides the analytical capability that differentiates humans from other primates.

The orthodromic maps begin as topological maps, exhibiting a topography that is a relatively faithful spatial representation of object space. The first of these maps is formed by the physiological optics at the retina. The next well known map is that formed in the LGN. A similar, although finer resolution map is formed in the PGN. Finally a medium resolution map is formed in the striate cortex. These maps have different functional requirements that help explain their difference in both spatial resolution and spatial fidelity. The striate cortex map is the last map that exhibits a direct (although highly distorted for a purpose) spatial relationship to object space.

The other "maps" in the visual system exhibit abstract properties that can only be loosely associated with object space. This applies specifically to the maps reported in areas 18-22 (V2, V3 & V4) which are discussed in the next section.

15.5.3.4.2 The major antidromic maps of the afferent sensory paths

While the orthodromic maps are similar in all chordates, the antidromic maps are quite different. This is particularly true between humans and monkeys. The antidromic maps reflect the organization of the feature extraction engines of the subject.

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[17]Sherman, S. & Guillery, R. (2001) Exploring the Thalamus. NY: Academic Press. Chapter VII

While various crude maps have been presented describing the putative visuotopic maps of V2, V3 & V4, these have been based on sparse probing of these areas (see **Figure 15.1.2-2**). From this probing, some authors have defined a local sign related to these areas. More recently, Sherman & Guillery have noted the multiple minute maps found in V2. These appear to be related to the engines defined by Malach, et. al. It is not clear whether each of these maps exhibits a "local sign" in the visuotopic sense. It is more likely that each of these maps will exhibit a "receptive field." However, as these minute maps appear farther from the striate cortex, it is likely their receptive field will not be definable in the spatial coordinates of object space. The signals associated with the engines at these locations within V2, V3 & V4 are in machine language. They are also time sensitive. They generally do not respond to fixed images on the retina and may not respond to short-term repetitive stimulation by the same image (the source of flicker fusion, critical flicker frequency, etc.). The gross responses obtained by probing will more likely be definable in terms of individual geometric features in object space.

15.5.3.5 The maps associated with the efferent signal paths

15.5.3.5.1 The major orthodromic maps of the efferent command paths

The most studied visual maps that might be called antidromic with respect to the afferent signal paths, are not related to the afferent paths at all. The signals in the SC/cerebellum couple are primarily responsible for the decoding of higher order (abstract) commands received from the pre-motor areas (generally area 6) of the *neo*-cortex and from the alarm channels of the *paleo*-cortex (the LGN's). Because of the location of the superior colliculus, it is clearly handling efferent signals received from the *neo*-cortex or from the abstract outputs of the LGN's (via the control point). These signals are orthodromic with respect to the efferent signal paths.

The commands received by the SC/cerebellum couple are in machine language. For those commands received from the LGN's, the signals only exhibit a coarse relationship to the spatial coordinates of object space. This relationship is further obscured by the fact that the machine language used in unknown to the research community. Our knowledge in this area is due primarily to traffic analysis in the language of the cryptoanalyst.

Note also that the superior colliculus is a volumetric neural organ. It does not have a sheet like surface with areas that can be easily correlated with similar areas of the retina.

15.5.3.5.2 The major antidromic maps of the efferent command paths

No significant studies could be found that related to antidromic maps of the efferent paths related to vision. There may, however, be some maps tracing the degree of rotation of the line of fixation (shared between the head and eyes) that results from stimulation of a given spatial region of the retina. This situation illustrates the fact that the efferent neural system does not respond directly to visual sensory input. All responses are based on abstract signals controlled by the control point (defined as the switching portion of the thalamic reticular nucleus in the next major section).

15.6 The role of the paleo-cortex in vision

A clear description of the role of the paleo-cortex is difficult to find in the vision literature. That in PART I is the broadest known to be available. This section will build on that model. The expansion will focus on the diencephalon. A later section will focus on the SC/cerebellum couple.

15.6.1 The topography, topology and commissure of the diencephalon

There are at least three functionally distinct parts of the diencephalon, describe either as the newest part of the old brain or the oldest part of the *neo*-cortex. The nomenclature depends primarily on ones teacher. The diencephalon is physically dominated by the thalamus. However, it has recently become apparent that the thalamus is largely enclose by a thin neurological shell. Because of its critical role with respect to vision, this work will treat the outer shell enclosing a large part of the thalamus, and generally known as the thalamic reticular nucleus, TRN, as a separate entity. This is because of a myriad of topographic and topological features that distinguish it from the rest of the thalamus.

It is critical to the discussion that follows to stress that;

> **The visual system of man begins to diverge significantly from the lower primates and other species near the pulvinar, the thalamic reticular nucleus (TRN) and the so-called perigeniculate nucleus (PGN) of the thalamic reticular nucleus. One cannot discuss the**

visual performance of man (particularly regarding reading and the analysis of fine detail) based on the writings applicable to these areas in lower animals.

The diencephalon stands at a crossroads in both the entire visual and entire neural systems. Yet its role in both systems is largely unknown. The role of the fornix, amygdala and thalamus are recognized as related to the well being of the organism, but their precise roles remain elusive. Tasker, et. al. provided a good description of the topography of the thalamus, related to its visual aspects, as they were known in 1982[18]. However, it is largely limited to knowledge gained through observation of behavior in response to lesions in animals, and probing with DC or simple AC signals. They note "Clinical neurophysiological observations on the visual pathways are few." Their discussion highlights the multitude of paths taken by the neurons of the optic nerve as they reach the thalamus and superior colliculus. The discussion focuses on clinical responses but does not address actual signaling or signaling paths. The lists provided are not necessarily consistent but they are informative. A similar discussion on the role of the vestibular-thalamic interconnections is also provided. However, this subject is beyond the scope of this section.

To interpret correctly the features of the diencephalon, understanding its physical complexity is important. This has been very difficult in the past and investigators have typically relied upon slicing the structure into thin layers along various planes to differentiate the various elements. Watson has provided excellent images using this technique[19]. However, the difficulty of displaying the thalamus and nearby structures in a single view is summarized in Nolte & Angevine (fig. 9-13, 2000). More recently the use of computer-aided 3-D reconstructions, and also three-dimensional computer-aided tomography of in-vivo diencephalons has provided a new level of understanding in this area. The reconstructions of Sundsten in Nolte are recommended. It is hoped they publish more in the near future. Their figures 16-1 and 16-21, -22 provide the best overall view of the diencephalon available. However, they do not show the fornix, amygdala or differentiate the TRN.

To highlight the portions of the diencephalon crucial to vision, the caricature of **Figure 15.6.1-1** is offered. The figure stresses the bifurcated nature of the thalamus with the corona radiata emanating upward from the internal capsule found between the two portions. A similar commissure radiation occurs from the bottom of the internal capsule where it is called the cerebral peduncle. It also stresses the morphologically and topologically unique nature of the two thalamic reticular nuclei that surround the upper two-thirds of the thalamus. They are shown moved to the left for clarity. An LGN is found at the lower right corner of both the foreground and background thalamic halves, with the MGN shown between them. A very significant fact is seen when the TRN is moved back into position over the thalamus. In this situation, the perigeniculate (PGN), a part of the pretectum, is found overlaying the LGN. In this configuration, the optic nerve is seen approaching from the left. The nerve bifurcates first at the conventional optic chiasm, labeled #1, in order to proceed down both sides of the thalamus. It then bifurcates again at the second optic chiasm, labeled #2, in order to terminate at both the LGN and the PGN. The PGN termination is shown crosshatched. This crosshatched portion contains the neurons from one semi-field from each of the foveola. These fields are merged in the PGN just like the peripheral semi-fields are merged in the LGN. While the LGN is shown with neurons of the optical radiation proceeding to area 17 of the cerebral cortex, the signals from the PGN/pulvinar couple proceed primarily, and directly, to area 7 of the *neo*-cortex.

> Although seldom mentioned in the literature, there are two medial geniculate nuclei and they obviously are not on the median. They are just closer to the median than the lateral geniculate nuclei.

In humans, the outside dimensions of the thalamus are about three centimeters along the rostral-caudal axis and about two centimeters vertically. The overall width of the thalamus is similar although a large void is found in its medial area containing the internal capsule. The TRN may have a thickness of 0.5 millimeters in some areas. This is somewhat thicker than the human retina and is suggestive of the multilayer neural complexity found within it.

The major elements of the precision optical system are shown along the bottom of the figure. They are connected serially to signals emanating from the pulvinar (lower right) region of the thalamus. The other structures shown are for context. The fornix is shown symbolically and also represents the amygdala. Like the TRN, the hypothalamus, fornix and amygdala are believed to be associated with controlling the very essence of the organism, its state of homeostasis and mental being.

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[18]Tasker, R. Organ, L. & Hawrylyshyn, P. (1982) The Thalamus and midbrain of man. Springfield, IL: Charles C. Thomas, pp 230-245

[19]Watson, C. (1991) Basic Human Neuroanatomy. NY: Little Brown

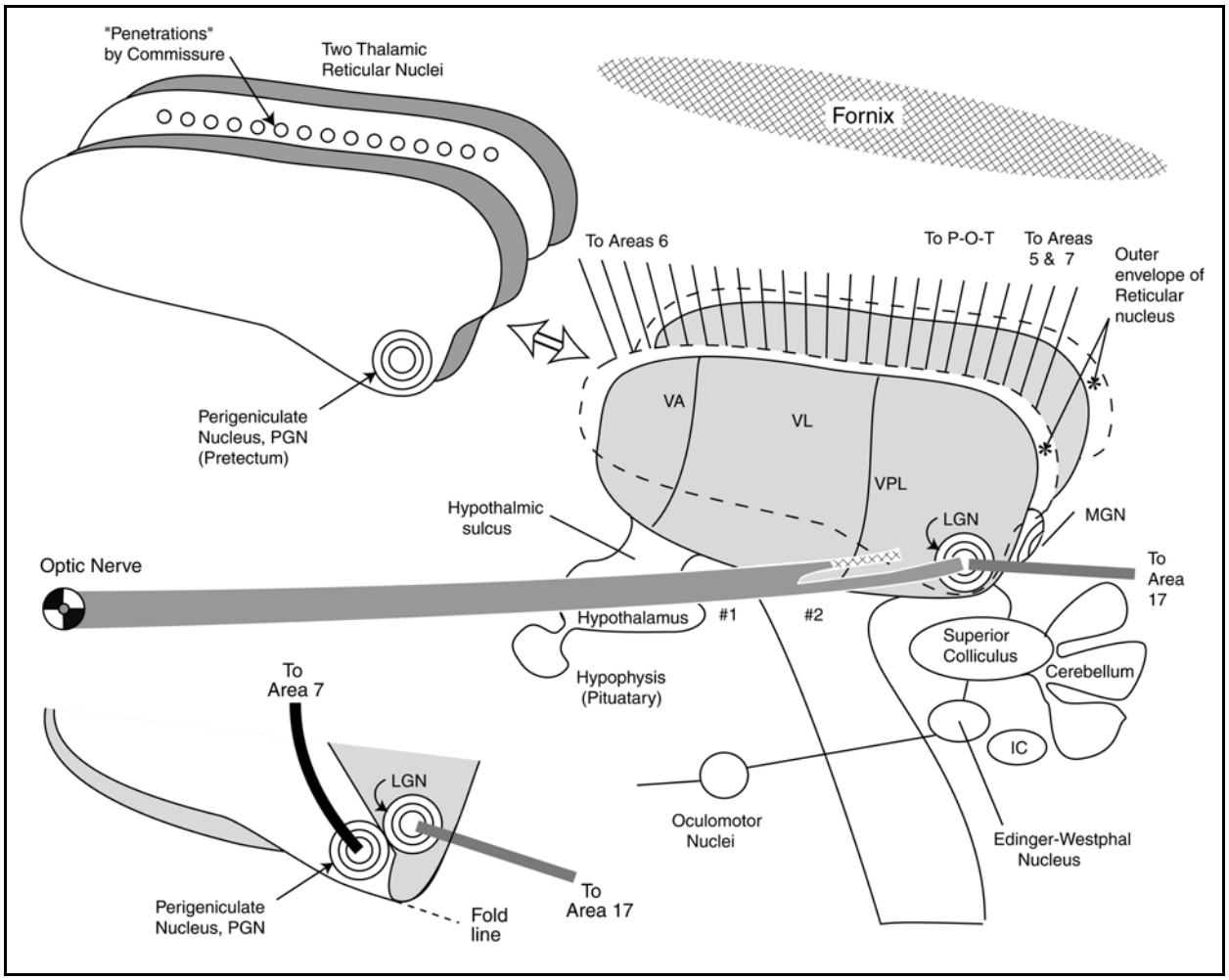

Figure 15.6.1-1 A caricature of the portions of the diencephalon crucial to vision. The two "sleeves" of the thalamic reticular nuclei, which may have significant thickness, are shown moved to the left to expose the thalamus and some of its nuclei. When in place, the perigeniculate nuclei on each side overlay the LGN's. The cross hatched portion of the optic nerve connects to the perigeniculate nucleus. The inset at lower left is suggestive of the formation of the TRN as an extension of the ventral thalamus. The PGN and LGN are then adjacent to each other and separated by a fold line. Not shown in this figure are the perireticular nucleus and intralaminar nuclei of the thalamus or the cerebral peduncle.

15.6.1.1 The role of the thalamus in vision and related activities

Sherman & Guillery have provided the latest major published work on the thalamus[20]. It is an excellent work. Their introduction is recommended. It develops the gestation period of such a work, beginning in 1986. Their preface echoes the remarks above. "The title of this book is intended to convey the sense that there is a great deal still unknown about the thalamus and that our aim in writing has been to show some of the major and minor roads, the footpaths, and the frank wildernesses that still need to be explored." They go on, "The thalamus, in terms of its detailed connectivity patterns, the functioning of its circuitry, and, perhaps most interestingly, its functional relationship to the cerebral cortex, is largely terra incognita." The use of the expression terra incognita has a long

[20]Sherman, S. & Guillery, R. (2001) Exploring the Thalamus. NY: Academic Press.

history in discussions of the thalamus, see below. They conclude with the note that "Knowledge of the thalamus is extraordinarily patchy." Their stated goals were "to look at many of the outstanding puzzles and unanswered questions that arise. . . ." and "move toward an understanding fo the possible role(s) of the thalamus in cortical functions. . . ." They have summarized these problems, as they perceive them in 2001, in lists at the end of each chapter. This work shares their goals and intends to provide more visibility into these roles through integration into a more detailed architecture, and a definitive description of how signals are processed within the various nuclei of the thalamus.

> Sherman & Quillery note that "The real truth is we wrote the book for ourselves . . . [and then] worked hard to make it accessible to others . . . It is probable that many of the ideas we present in this book will prove wrong . . . Whether they are right or wrong, we have attempted to make them stimulating." This methodology and approach have been shared by this author. They go on to quote Kuhn, quoting Francis Bacon, "**Truth emerges more readily from error than from confusion**."

The Sherman & Guillery work is light on detailed cytology. Steriade, Jones & McCormick are the definitive authors in this area as of 1997[21]. Their work on the thalamus is one of the few that discusses the internal organization of this three-dimensional structure. It opens entirely new avenues of interpretations based on the participation of the internal lamina of the thalamus. Because of the currency of the referenced research, many recent articles and books conflict with their terminology and claims.

15.6.1.1.1 Terminology associated with the thalamus

This work will begin to deviate from the concepts of Sherman & Guillery with terminology.

> 1. Their definition of "drivers" and "modulators" in their 2001 book, like that of FO and HO signals in their 1996 paper, is too restrictive. It forces them into a global definition of efferent and afferent neural channels. Thus they define drivers in terms of first order, or sensory, signals (signals that the cortex has not seen before). Modulators are defined as higher order signals (generally originating in the cerebrum and being passed via the thalamus to other cortical areas). Such a concept is difficult to support within the cortex (see their page 245) where the various engines are connected through a general purpose star network. In such a network, all engines are capable of communicating directly with all other engines (see earlier discussions in **Section 15.2.2**). Sillito & Jones have also argued for a broader interpretation[22]. This work will speak of signaling channels and supervisory channels. Each of these channels can be considered afferent or efferent with respect to a given engine. However, the channels themselves may not have a directional significance. In this sense, a sensory signal is an information signal ascending in the general sense. Similarly, a command signal initially generated within the cerebrum, for purposes of skeletal motor control, is also an information signal but it is descending in the general sense. The drivers of Sherman & Guillery can be considered to travel over, or be, information signaling channels (page 18). The operation and switching of these signaling channels are controlled by supervisory signals that can be thought of as modulators in a primitive sense. In the more general case, a supervisory signal is a complex vector just like most information signals. A single supervisory signal may involve multiple neural paths, operating in parallel, to transmit the complete supervisory message. In addition, a single message may cause several actions at different points along its supervisory path. A new supervisory signal may be created by any engine by extracting information from the information signals it is processing. Later, they attempt to correlate their drivers and modulators with specific characteristics such as receptive field and signal duration. However, they did not develop a clear description of the fundamental difference between tonic and phasic signaling. Their summary of the scope of, and limitations on, their definitions of drivers and modulators are informative and important (pg 261). On page 264, they briefly introduce a third or subsidiary type of signal which they give the name of "disrupter." On page 265, they note the tentative, and largely unverified, nature of their drivers and modulators. Hopefully, a clearer picture will emerge from the combination of their work and this work.
>
> 2. The arbitrary division of signals related to the thalamus into relay and association types (found frequently in the literature) will not be supported here. The concept is too elementary.

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[21]Steriade, M. Jones, E. & McCormick, D. (1997) Thalamus, vols 1 & 2. NY: Elsevier, pp 55-72

[22]Sillito, A. & Jones, H. (1997) Functional organization influencing neurotransmission in the lateral geniculate nucleus. *In* Striade, M. Jones, E. & McCormick, D. Thalamus, vol. 2. pg. 1

3. Sherman & Guillery concentrate largely on cyto-architecture and tecto-architecture. Their discussion of signaling architecture is limited largely to first order traffic analysis–where do association neurons originate and terminate and what commissure do they follow to reach their terminal points. With a more comprehensive model and architecture of the signaling system, considerable progress is possible in defining the roles of the thalamus more fully. This additional definition is a goal of this section.

15.6.1.1.2 Architectural interpretations

This work will differ from Sherman & Guillery further in architectural interpretation where they draw a corollary on page 8. They say, "If the thalamus acts to control the way that information is relayed to the cortex, then it may be a mistake to look for it to act as an integrator of distinctive inputs as well." There are many powerful feature extraction engines in the thalamus. They can accept a multitude of simultaneous and distinctly different roles simultaneously. Their comment that "At present the most detailed information available on thalamic relays shows that information from the ascending pathways is being passed to the cortex without significant change in 'content'." is not compatible with the extensive work of Livingstone & Hubel that they address later in the work. Maybe that is the reason for their quotation marks around the word content.

Tasker, et. al[23]. give a review of the electrophysiological literature concerning the visual pathways afferent to the thalamus and efferent from the thalamus. As expected, agreement is hard to find when combining morphology and commissure. They find about six discrete termini on the thalamus for various parts of the optic nerve. These include the accessory optic tract (Precision Optical system of this work), optic tectum, pretectum, LGN's, etc. They also document the generally accepted two paths from the thalamus to the cerebrum, via the geniculo-calcerine pathway and the tecto-pulvinar paths. They note the independence of these paths, even speculating on their common historical origin. They also noted the surprising inability, in the absence of any internal thalamic structure or alternate pulvinar pathways, to disrupt the visual pathways by super cooling the LGN's.

Sherman & Guillery also note the frequent distribution of the same axonal signal to multiple cyto-architecturally distinct areas within and exterior to the thalamus (pages 43-44). This is another example of the importance of the thalamus beyond the simple relay role.

1. While they maintain the cell structure, within the thalamic reticular nucleus, is well studied[24], this work will attempt to define the TRN further. The main part of the nucleus can be divided into compartments, based on the commissure associated with an area. However, there are no morphologically defined borders (architectonic distinctions) and very little definition of the limits of the regions associated with different modalities.

The last chapters of Steriade, et. al. vol. 2 provide considerable information on diseases of the thalamus. This material is outside the scope of this work.

2. The conventional wisdom, as discussed by Sherman & Guillery, is that the thalamus is highly involved in two functions, the relay of information between two end points and the association of signals passing through the thalamus. The structure supporting these operations involves many "nuclei." This work takes a broader view. Each nucleus is considered to contain one or more feature extraction or command generation engines. There is no necessity to commit about a billion neurons, in multiple feature extraction engines, to perform the roles of relay and association in the sense they are commonly used in the literature.

In this work, a broader view is taken and will be elaborated upon. The thalamus is considered a major signal processing and interpretation center, performing major degrees of feature extraction related to visual images and other modalities. It is also considered to house a major switching operation that combines the awareness, alarm, analytical, vestibular and volition modes of operation in a complex way under established and learned rules of precedent and priority. These actions are carried out by major engines that exhibit little direct correlation to the topography of the thalamus. They are actually in the TRN. In this work, **the thalamus is not only the gateway to the cortex, it is the gatekeeper (and traffic officer)** for nearly all afferent and efferent signals of the nervous system.

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[23]Tasker, et. al. (1982) Op. Cit. pp 230-233

[24]Sherman, S. & Guillery, R.. (2001) Op. Cit. pp 54-58

3. Sherman & Guillery have adopted the term tonic to describe the output waveform of a free running oscillator. This is in considerable conflict with the rest of the physiological community. It will cause difficulty when describing the output of individual analog neurons within the engines of the CNS. While the physiological identification of individual analog neurons may be difficult with current protocols (Sherman & Guillery, '96, pg 1375), future progress requires such identification. As noted in **Section 15.1.4.10**, the term tonic will be reserved for a DC or slowly changing analog waveform absent any oscillatory component. McCormick, et. al. describe a "rhythmic burst" that appears to describe the free-running oscillation causing a stream of action potentials.

The gatekeeper role is stressed in the suggestion by Sherman & Guillery that "whatever the thalamic nuclei do for the major ascending pathways, it is likely to be doing something very similar for corticocortical communications." This is the role of a gatekeeper. It is similar to the two-way function of a railroad marshaling yard. In this work, this gatekeeper, marshaling yard, or whatever, is called a control point until its physical location, or extent, can be defined more completely.

This broader role is in consonance with prediction by Sherman & Guillery (pg 7) that "it is probable that more than one functionally significant mechanism will be apparent once we have a clear understanding of these aspects of thalamic organization." It is also compatible with their observations (Chapter VI & IX) that the role of the relays may change in relation to different behavioral and attentional states. Their pages 240-245 also address this question, but within the narrow context of their drivers and modulators.

15.6.1.1.3 Relative sizes in the elements of the diencephalon

Recently, research has begun to elucidate the major role of the pulvinar in human vision. Robinson & Cowie state; "The pulvinar complex represents the largest mass within the primate thalamus and contains more neurons than any other thalamic region. Its expansion has nearly kept pace with the growth of the cerebral cortex during the phylogenetic development of apes and man. In comparison, the lateral geniculate nucleus (LGN) is considerably smaller but, probably because of its direct retinal relay to the primary visual cortex, has received a great deal more attention from investigators."[25] They go on to state their theme, which is shared with this work, " . . . the pulvinar is organized to contribute signals which indicate the salience of visual images and events." They go on; "However the saliency of visual events is determined, it is our hypothesis that the pulvinar plays a critical role." It will become apparent in this section, that the pulvinar, in association with the perigeniculate nucleus, of the larger thalamic reticular nucleus, play the initial role in determining the interp(s) defining the saliency of the image projected on the foveola. The remainder of their presentation is insightful, although their terminology appears to vary from that used by the majority. Jones provides a broad translation table concerning the thalamus[26]. Unfortunately, it focuses on the ventral portion. Macchi & Jones have provided additional nomenclature[27].

Statements have been made that the thalamus of man is approximately 5-6 times the size of that in monkeys. Such a statement needs additional consideration. Figure 1 in Sherman & Guillery shows the difference in cross-sectional area of the thalamus between man and an unspecified monkey to be different by a factor of sixteen. However, the thalamus is a three-dimensional structure. More importantly it is largely filled with neurons (as opposed to the cerebrum that consists of a thin folded sheet of neurons). The volume of the human thalamus, based on the above figure and assuming the thalamus is largely ellipsoidal in both cases, is closer to sixty-four times the volume of that of a monkey. Since neurons do not scale significantly, this means, the number of neurons in the human thalamus is approximately sixty-four times that of a monkey. This ratio represents a fantastic increase in neural processing power.

The above ratio may be even higher based on the observation of Robinson & Petersen that the pulvinar has been one of the largest contributors to the growth of the thalamus[28]. This would imply that the growth of the pulvinar may have been disproportionately greater than the growth of the thalamus. Such disproportionate growth also appears to be present in the exterior shell of the thalamus, known as the thalamic reticular nucleus, TRN. It appears that this structure begins to grow disproportionately in the primates. Its presence is minimal in the rabbit, more obvious in the cat, and progressively more prominent in the prosimians, simians and finally man. This subject will be developed further in **Sections 15.6.1.3** & **15.2.5**.

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[25]Robinson, D. & Cowie, R. (1997) The primate pulvinar: structural, functional, and behavioral components of the visual salience. *In* Steriade, M. Jones, E. & McCormick, D. Thalamus, vol. 2, NY: Elsevier. pg 53-54

[26]Jones, E. (1997) in Steriade, et. al. vol. 2, Op. Cit. pp 480-483

[27]Macchi, G. & Jones, E. (1997) Towards an agreement on terminology of nuclear and subnuclear divisions of the motor thalamus. *J. Neurosurg*. vol. 86, pp 670-685

[28]Robinson, D. & Petersen, S. (1992) The pulvinar and visual salience *TINS*, vol. 15, no. 4, pp 127-132

15.6.1.1.4 Some reported functions of the thalamus

While from a different perspective, the literature reports three states of thalamic function. These are the relay function, the ability to change its functional state, and the integrative function[29]. The first is generally associated with the LGN. A broader view is taken here that includes signal extraction as well as image merging. The second is broadened here and associated with controlling the switching portion of the TRN. The third is expanded to include a correlation capability that is key to the extraction of features in a scene.

15.6.1.1.5 Capabilities required of the thalamus in vision

Two functional capabilities appear to be required of the thalamus. The morphological location of these capabilities has not been previously documented. As shown in the expanded top level schematic of the human visual system, [**Figure 15.6.1-1**], these capabilities relate to two areas. The first is the initial conversion of images of symbols projected on the foveola into interps that can be processed further by subsequent parts of the visual system. The second involves the control of the operating modes of, and the distribution of signals generated within the cortex related to, vision. It appears that the morphological areas related to these functions can now be documented to a considerable extent.

The control requirement calls for a significant dynamic switching capability. Such a capability goes well beyond that of a relay center. The capability requires its own associated engine to evaluate various instructions (that may be in conflict) and a memory to store the available options.

The conversion of the features of imagery into "machine language" vectors demands that a highly capable correlation mechanism be available that is supported by a significant memory capability. To be effective, the memory must be compatible with a learning process. This requirement suggests it must be expandable, changeable and update-able. Such a memory can be considered of the random access type. However, based on experience, it is suggested that it be of the write-once, read-repeatedly type, e. g., a programmable read-only memory (PROM).

The question becomes, can such capabilities be found within the thalamus?

15.6.1.1.6 Operationally crucial location of the Thalamus

For the same reason that the head is at the front of four legged animals, operational requirements are key to the location of the thalamus, and particularly of the thalamic reticular nucleus. The velocity of neural signals is relatively limited. To operate efficiently (avoid being eaten and/or catch prey), it is important that the central control point of the visual system exhibit the shortest possible distance between the location of the eyes, the decision making center and the musculature controlling the pointing of the eyes. Similar requirements exist for the operational capability of reading.

As an example, consider the time delay involved in the POS servomechanism controlling the eyes. An initial estimate of the total loop delay of the Precision Optical System is approximately 50 ms. If the *neo*-cortex were involved in this loop, the delay in signals merely reaching Area 17 from the retina would be longer than 50 ms. The total loop delay would be more than 100 ms. Not surprising, the *neo*-cortex is not involved in the most time critical operations of the visual system. Instead, the elements of the thalamus are provided prioritized instructions in advance, which they store. In operation, the thalamus operates as the hub of the visual system. Its thalamic reticular nucleus is the actual control point. It controls and performs a variety of tasks, only referring to the anterior lobe of the *neo*-cortex when an event occurs that is outside its stored instructions.

It will become clear below that the elements of the thalamus rely upon detailed stored instructions and lookup tables to avoid the time-consuming calculations required in their absence.

Thus the thalamus is placed as close to the eyes as possible, is provided with independent authority to react (based on prioritized instructions) and is provided with the required memory and switching capabilities to perform a wide range of calculations. Because of these capabilities, it is the thalamus that is most appropriately labeled the "primary visual cortex." However, that label has become entrenched in the lexicon of vision by history. Maybe the "ultimate visual cortex" will come into use.

The superior colliculus and cerebellum are located as close to the thalamus as possible since their performance is

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[29]Steriade, M. Jones, E. & McCormick, D. (1997) Thalamus, vol. II. NY: Elsevier pg 543

critically important to the overall time delay of the POS servo loop. The elements of the visual system that are less time critical to the operation of the visual system, such as the lobes of the *neo*-cortex, are located at a distance from the thalamus.

15.6.1.2 Important features of the Thalamus

The diencephalon has been defined primarily in terms of its gross morphology and topography. Carpenter & Sutin provide a broad discussion of the thalamus that is unfortunately light on its visual aspects[30]. This may be due to the highly transient role of the signals in the thalamus related to foveal vision. It may also be due to the overwhelming amount of data now emanating from the group of researchers led by Guillery. They originally divided the diencephalon into four major parts based on Jones and the much earlier work of Rose, the epithalamus, the dorsal thalamus, the ventral thalamus and the hypothalamus.

As discussed below, the thalamus remained largely a "terra incognita" up through 1985. Because of this, the discussion in this work must be considered more speculative than earlier sections. However, the data is beginning to present a compelling picture that cannot be ignored. The epithalamus is now being explored under the designation, thalamic reticular nucleus, TRN. The exact morphological origin of this element is not clear. It appears to emanate from the ventral portion of the thalamus but also to have a very close relationship with the limbic system.

Topology, the tracing of the interconnections and identification of individual circuit nodes within a structure, has been a priority in the work of the Guillery group. They have shown that the thalamus play many critical roles, and not only in vision. These roles do not exhibit a one-to-one relationship to its topography. One must be careful when isolating a function and assigning responsibility for that role to a specific morphological feature.

15.6.1.2.1 The Pretectum subdivides into the PGN and Pulvinar

Up to this point, a crucially important role in chordate vision has been described as a conceptual spinoff of the LGN known as the pretectum. While the term has been used commonly with respect to lower chordates, it has not been common in investigations of primates and humans. In the following discussions, the pretectum will be defined in greater detail. It will be shown to receive signals over part of the optic nerve from the foveola and consist of (at least) a two-dimensional correlator (the perigeniculate nucleus) and a large lookup table (part or all of the pulvinar). It will also be shown that these elements are critically important in the analysis of fine detail and the related skill of reading. It appears that the size of the pulvinar is directly related to the level of development in these skills among species.

While the term pretectum may appear in the following text, it should be understood this is a conceptual label encompassing the above structures. When discussing their close functional ties, the combination of the PGN and the pulvinar will be described as a PGN/pulvinar couple.

15.6.1.2.2 Coordinates and labels

As elsewhere in vision, few authors use the same terminology when discussing the various nuclei of the thalamus. The terminology used by Carpenter & Sutin has been largely superceded by the broader and more consistent terminology of the Guillery group[31 ,32]. Because of these features, it is this terminology (based on Jones, 1985) that will be adopted here. It will occasionally be enhanced by the terminology of Conley & Diamond when discussing the LGN[33] and Nolte & Angevine when discussing the more global aspects of the brain[34].

There is a major need for more investigators to adopt the stereotaxic procedures used by the Guillery group. This is particularly important when investigating the TRN and pulvinar. When a typical engine of a million neurons occupies an area of only a few square millimeters, and adjacent engines are spaced accordingly, it is absolutely necessary and differentiate precisely between the areas (and engines) of the thalamus. With the individual features of the thalamus found to vary by a millimeter or more between individuals of the same species, precise stereotaxy is needed just to correlate the topological data in the various data sets.

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[30]Carpenter, M. & Sutin, J. (1983) Op. Cit. pp 500-528

[31]Sherman, S. & Guillery, R. (2001) Op. Cit.

[32]Lozsadi, D. (1995) Organization of connections between the thalamic reticular and the anterior thalamic nuclei in the rat *J. Comp. Neurol.* vol. 358, pp 233-246

[33]Conley, M. & Diamond, I. (1990) Organization of the visual sector of the thalamic reticular nucleus in *Galago*. *Euro. J. Neurosci*. vol. 2, no. 3, pp 211-226

[34]Nolte, J. & Angevine, J. (2000) Op. Cit.

Globally, and particularly after the TRN has been removed, the thalamus appears to be a unitary structure that retains a high degree of bilateral symmetry with respect to both its inputs and outputs. A major question is how much of its internal structure is unitary in goal and design, although some duality may be preserved for purposes of redundancy? Most intermediate level texts and articles do not address the fact that the thalamus is a three-dimensional structure. It includes internal engines as well as commissure.

With respect to vision, the thalamus is usually subdivided into bilateral pairs of "nuclei," the two LGN's, two perigeniculate nuclei, two pulvinars, etc. Interestingly, it is frequently described as having only one median geniculate nucleus. However, it is usually pictured as having two. The connotation of the name is not helpful in this regard. More important, the thalamic reticular nucleus enshrouding the thalamus exhibits a very complex structure that is difficult to map.

15.6.1.2.3 Gross morphology of the Thalamus related to vision

Nolte[35] has provided a tabulation of the morphological subdivisions of the thalamus and their alphabetic abbreviations. Although incomplete, Nolte has also provided a list of interconnections to the thalamus in his Table 16-2. His definition and classification of "relay" as used in that table are not supported by this work. His discussion accompanying the table speaks of the more complicated task of data merging within the thalamus.

Carpenter & Sutin have supplied an excellent caricature of the thalamus as of 1983. The figure stresses its interconnections with other cortical elements[36]. The figure is color-coded to show connections with similarly color-coded internal and external profiles of the human cerebrum. Unfortunately, the caricature does not represent the shape of the thalamus, does not show the thalamic reticular nucleus, and the connections are only shown conceptually. They note specifically the connection of the areas labeled VPM and VPL with area 7 of the cerebrum via the Pulvinar pathway (although the figure stresses the equally important connection of these areas with the cerebellum via the trigeminothalamic tracts). The VPM is the ventral posteromedial nucleus. The VPL means the ventral posterolateral nucleus. These bodies are also known by a variety of other names. They also note the connection of the VPM with the frontal areas, 3, 1 & 2 (listed in that order). These may only be connections via area 7.

Noback has also noted the participation of the ventral lateral nucleus, VL, in the signaling loop consisting of the cerebral cortex to the cerebellar cortex and back to the cerebral cortex[37]. This loop is discussed in terms of the primary role of the cerebellum as a long term read-only memory in **Section 15.2.2.7**.

The thalamus consists of two major morphological elements, the thalamus and its unique covering, the thalamic reticular nucleus. Until about 1980, the TRN was largely overlooked. Since then, recognition of its critical importance has grown by the day. This section will provide a brief overview of the morphology of the thalamus before a more extensive discussion of its electrophysiology.

The description of the thalamus and TRN is difficult because of their unusually convoluted shapes. While the TRN essentially covers at least two-thirds of the thalamus, this cover is not like the hide of a baseball. The thalamus is a nearly bifurcated structure, similar to the thyroid gland, where each of the wings has a complex structure. Between the two wings is a very complex plexiform, the internal capsule, where many commissure converge from all parts of the brain. This plexiform is so complicated in shape that it has been given two names, the coronal radiation for the part that can be viewed dorsally and the cerebral peduncle for the part visible ventrally.

The TRN is nominally a 0.5 mm thick sheet of neural tissue that acts as a transit point for (probably) all neurons entering the thalamus. However, it does vary in thickness, and does insert itself into nominally interior spaces of the thalamus. Because of the physical distances involved, there are commissure between the TRN and the thalamus proper. At the detailed level, there are many distinct neural arrangements (engines) within the TRN. These arrangements are so structured that they affect the external appearance of the TRN. The surface of the TRN is quite complex in appearance. Some areas appear relatively smooth while other areas appear reticulated or striated. In this context, a reticulated surface appears as if woven with threads traveling in multiple directions. A striated surface appears corrugated with the dominant pattern traveling in only one direction.

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[35]Nolte, J. (1999) Op. Cit. Chap. 16

[36]Carpenter, M. & Sutin, J. (1983) Human Neuroanatomy, 8th ed. Baltimore, MD: Williams & Wilkins, pp 500-515

[37]Noback, C. (1967) Op. Cit. Chapter 9 and pg 203.

The thalamus is not formed from a thin sheet of neural tissue like much of the cortex. Each of its bifuracted lobes is a three-dimensional mass of neurons. The maximum dimension of one of these masses is over three cm. in humans. In this respect, it is similar to the superior colliculus. These volumetric structures have made it difficult for electrophysiologists to define their roles precisely. Most reports merely establish a causal relationship between excitation of the retina at a given location and the response at a given location within the thalamus. These responses generally represent the receptive field of the neuron rather than a projection of the retinal image.

Lacking significant surface markings and being located in such a confined place, a variety of investigators have attempted to draw and photograph the thalamus from every angle. The figure in **Section 2.3.1** provides a global view of the old brain. However, it does not provide the detail necessary for this section. Nolte and Nolte & Angevine have recently provided the most exhaustive photographic study of the thalamus and its related structures. Their figures do not address the cerebral peduncle emanating from the ventral external surface of the thalamus. They show a massive coronal radiata emanating from an external surface. Other drawings treat this area as if it was a cutaway showing the coronal radiata emanating from the inside of the bifurcated thalamus and the cerebral peduncle exiting at a ventral location. Still other drawings show an additional plexiform, generally labeled the perireticular nucleus, associated with the lateral surfaces of the thalamus. Further definition and spatial precision are needed in interpreting this area.

As discussed above, the internal capsule is a large mass of axons emanating from the thalamus (via the TRN) that breaks into a series of commissure going to a wide variety of area of the cerebrum. While a few target areas in the cerebrum can be specifically labeled, some axons go to and return from almost every named area of the *paleo*-cortex and every numbered area of the *neo*-cortex. Nolte points out that no neurons from the areas within the thalamus that are labeled project to the cerebrum without passing through a part of the thalamus called the thalamic reticular nucleus.

Figure 6-8 of Nolte & Angevine is particularly important in confirming the optic nerve terminating in an area where the pulvinar, pretectal area, superior colliculus and the brachium of the superior colliculus come together. Only detailed probing can confirm which neurons from the optic nerve terminate where. Gross lesions have been used to provide the general nature of these terminations (See **Section 2.8.1**). A similarly definitive figure showing the physical relationship between the termination of the optic nerve at the lateral geniculate nucleus and the origination of the optic radiation has not been found. The size of the LGN makes it unlikely that all of the neurons associated with vision originate and terminate within the area normally described as the LGN.

Exactly how these commissure intercept the thalamus is another question. Generally, commissure connecting to the cerebrum and cerebellum approach these bodies from the inside (layer 6) of the neural sheet. Does the outer surface of the volumetric thalamus correlate to layer six of these other bodies or do the various commissure enter the thalamus and then interconnect with an inner surface?

The pulvinar is the label assigned to the most caudal (posterior) portion of the thalamus. It is highly involved in the visual process. However, how it is involved has long been a matter of conjecture. Nearly every neuron within the pulvinar has a large receptive field when referred to the retina. It is the prime candidate for providing the large scale lookup table required by the control point and the POS of the visual system.

15.6.1.2.4 The detailed topography of the thalamus related to vision

Because of the more extensive investigations carried out in monkeys and cats, more is known of the role of the engines of the thalamus in these species. Currently, the most studied parts of the thalamus relating to vision are the lateral geniculate nuclei (LGN). However, Sherman & Guillery note that only 10-20% of the neurons in the LGN are directly related to either input or output commissure related to vision. This suggests a role broader than switching for these engines (nuclei). In this work, the other 80-90% is involved in computation. This level of computation is associated with two goals. These are the merging of images for purposes of generating supervisory signals useful in stereopsis, and in alarm mode signal generation. This greater degree of complexity than required for relaying is seen in all of the thalamic engines (nuclei).

Most of the available caricatures of the thalamus strip away the jacket-like portion known as the thalamic reticular nucleus (TRN) to simplify the discussion. This action is catastrophic with regard to understanding the neural (and visual) system. The TRN (frequently abbreviated to R in illustrations) is one of the most important convergence points in all of the brain. **Figure 15.6.1-2** shows the relationship between this jacket and the remainder of the thalamus of the macaque monkey. The three drawings from a camera lucida are in posterior order[38]. The top view

[38]Hunt, C. Pang, D. & Jones, E. (1991) Numbers and proportions of GABA immunoreactive neurons in intralaminar and relay nuclei of the monkey thalamus *Neurosci*. listed as in print. xxx

shows the TRN along the side of the lateral posterior nucleus, LP, and near the ventral posterior lateral nucleus, VPL. The area between them contains commissure. The perigeniculate nucleus (Pg in this figure) is shown separately from the dorsal lateral geniculate nucleus, Lgd. Benson, et. al. provide two actual photographs of the LGN/PGN relationship from which Hunt worked[39]. They show the PGN overlaying, but distinct from the LGN in one slice and moving away from the LGN in the other. The first slice clearly shows part of the optic nerve sandwiched between the LGN and PGN. The second, stained for GABA (presumably using their GAD sensitive chemistry) shows a remarkably uniform appearance within the LGN and the PGN but little staining of the optic nerve.

The middle view shows the perigeniculate nucleus as a "cap" on the LGd and the TRN wrapping the entire side of the thalamus. Large areas between the elements are occupied by commissure. Because of this cap arrangement, authors do not always differentiate between neurons of the optic nerve passing to these elements individually. As noted by McCormick, et. al., "neurons in the perigeniculate nucleus display morphological, anatomical, electrophysiological and pharmacological responses which are either identical or nearly identical to those of cells in the TRN." This suggests that the PG is actually an extension of this nucleus. This distinction will become more significant

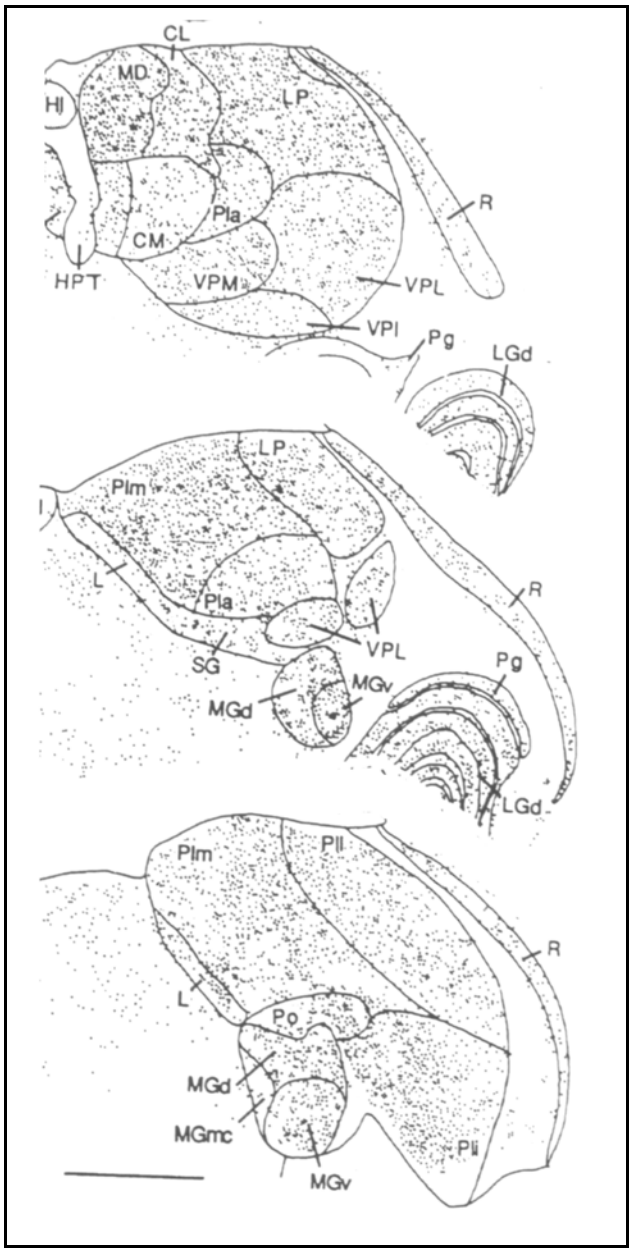

Figure 15.6.1-2 Three sections through the thalamus of monkey. Scale bar is 500 microns, 0.5 mm. See text for discussion. Modified from Hunt, et. al. 1991.

[39]Benson, D. Isackson, P. Hendry, S. & Jones, E. (1991) Differential gene expression for glutamic acid decarboxylase and Type II calcium-calmodulin-dependent protein kinase - - *J. Neursci*. vol. 11, no. 6, pp 1540-1564

below.[40] It is related to the embryology of the diencephalon.

The lower view shows the TRN continuing to enshroud the lateral pulvinar nucleus, Pll and the inferior pulvinar nucleus, Pli. Thus, the thalamic reticular nucleus enshrouds most of the sides of the thalamus in the monkey.

Jones has provided a series of photographs of the much larger human thalamus[41]. The TRN is frequently a full millimeter thick in these figures. The PG is also shown as a cap, wrapped on top of the LGd as in the above figure.

As noted by Cooper, et. al., the pulvinar is far more developed in man than in any other species and it shares connections with the retina and the cerebral cortex independent of those related to the LGN's.

15.6.1.2.5 Unique topological locations within the Thalamus

The thalamus is in a unique position with respect to the transmission of time sensitive visual information. Although not generally realized, the signals arriving (and leaving) the thalamus are not in time synchrony. The optical radiation, clearly a feature devoted to correlating the timing of the signals leaving the thalamus, is well known. Lesser well known is the similar radiation of the ganglion axons within the retina. Because of the group velocity of neural signals, this radiation introduces a variable delay in the signals of the optic nerve with respect to their point of origin in the retina. This delay is nominally proportional to the distance from a specific ganglion of the retina to the optic disk (lamina cribosa). It is not directly proportional to the distance of the stimulus from the point of fixation in object space.

The asymmetry, in the arrival time of signals from the peripheral retina, at the LGN of the thalamus is significant. It provides the capability of determining the time delay related to features in object space without employing specific time delay circuits in the thalamus.

Great strides have been made in understanding how the two LGN's spatially interdigitate the visual signals from the two eyes. However, no references were found in the literature to a similar interdigitation (or offset of the spatial data) with respect to time. By combining the interdigitation processes and employing simple correlation circuits in the signal manipulation process, the thalamus is in a position to extract several types of important signals. These include the signals necessary to (1) command the oculomotor system to correct for parallax errors between the two eyes, (2) provide tags to the data projected to Area 17 that represent the stereoptical range to features in object space, (3) and aid in the merging of the data from the two eyes in Area 17.

Meyer's loops introduce a significant time delay in the neural paths to Area 17. It appears this time delay is designed to compensate for the variable time delay introduced by the optical radiation within the retina. Oyster has illustrated this optical radiation[42]. Except for the asymmetries in the signal projection stage, this compensation brings the information regarding features in object space back into synchronism.

The medial geniculate nucleus, MGN, of the auditory system was shown in the above figure to emphasize the spatio-tempero-integration function of the thalamus. The data of the auditory system originates in two separate sources and requires integration similar to that of the visual system. The data must be correlated with respect to inertial space and time. Sensory systems, such as taste, smell and the more mundane somatosensors do not require the same degree of spatio-tempero-integration.

15.6.1.3 Major commissure in and around the diencephalon

The commissure surrounding, as well as internal to, the diencephalon have the complexity of a cable tray in a telephone central office. Describing the arrangement of these commissure is particularly difficult because of the complex shape of the thalamus. To date, the best figures applying to these commissure are probably from Nolte & Angevine. However, the black and white pictures and reconstructions cannot differentiate between and illustrate the complex bending of the major commissure at the detailed level. It can be hoped that a future figure, similar to theirs but color-coded as in those of Carpenter & Sutin, will appear.

Hassler defined six major divisions in the commissure associated with vision and the diencephalon in 1972[43]. He

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[40]McCormick, D. Huguenard, J. Bal, T. & Pape, H. (1997) *in* Steriade, M. Jones, E. & McCormick, Thalamus, vol. II, pg 159

[41]Jones, E. (1997) *in* Steriade, et. al. vol. II, figure 9.1

[42]Oyster, C. (1999) Op. Cit. pg. 195

[43]Hassler, R. (1972) Hexapartition of inputs as a primary role of the thalamus. *In* Frigyesi, T. et. al. *Eds*. Corticothalamic projections and sensorimotor activities. NY: Raven Press. Pp 551-579

lists them as:

1. The primary optic tract projecting to the lateral geniculate.
2. A first integrative path to the intergeniculate-pulvinar area.
3. A second integrative path with input to the lateral pulvinar.
4. A multisensory path to the medial geniculate.
5. An unspecific projection to the pregeniculate nucleus.
6. Projections to the reticular nucleus around the lateral geniculate.

Tasker, et. al. provided a discussion involving some of Hassler's paths and the paths defined by several other investigators (pg 230-33). While informative, the discussion appears largely out of date. This is primarily because of the limited ability to determine the precise paths and directions of signals achieved more recently with staining and autoradiographic techniques. Tasker also provides a considerable list of sensations observed when various areas of the *paleo* and *neo*- cortex are stimulated electrically with simple (irrelevant with respect to the machine language of the neural system) pulse signals. The list generally includes phosphenes (mostly white), hallucinations of objects moving in object space and obscurations of objects in object space.

These paths can be correlated with the paths discussed in this work (with only a few changes in nomenclature). This is best done by defining recognizable concentrations of commissure near the thalamus. The peri-reticular nuclei are found on the two lateral sides of the thalamus. The major concentration is found between the two wings of the thalamus and is generally labeled the internal capsule. The complexity of the internal capsule suggests a further subdivision of the internal capsule. One major commissure interconnects the two wings of the thalamus. This major commissure is labeled the corpus principia. A group of commissure leaves the internal capsule dorsally. These are conventionally called the coronal radiata. They connect with many engines within the CNS. Those related to the visual system generally connect with the parietal-occipital-temporal junction. Another group of commissure leaves the internal capsule ventrally. The largest group of these is conventionally described as the optical radiation. Most of the neurons in this commissure interconnect with the occipital lobe of the cerebrum.

15.6.1.3.1 Features of the internal capsule, the Corpus Principia

Nolte has defined five major parts of the internal capsule based on morphology[44]. Mitrofanis & Guillery have provided a more useful description based on the termination points of the various commissure entwined within the internal capsule[45]. The operational significance of these commissure suggest that the internal capsule contains another element. As discussed above, this element could be called the Corpus Principia based on its critical role in passing information between the two lateral halves and the medial portion of the thalamus. **Section 15.6.4.1** and [**Figure 15.6.4-2**] shows the critical functional role and physical position of the corpus principia in relation to the rest of the visual system.

15.6.1.3.2 Features of the peri-reticular nucleus (plexiform)

Mitrofanis & Guillery have described an additional area of commissure concentration that they have defined as the perireticular nucleus (in conformity with common morphological practice). This area is found along the external surfaces of the thalamus, outside the TRN. It appears a more appropriate functional name would be the perireticular plexiform (since the number of neural soma present is small).

15.6.1.3.3 Commissure internal to the diencephalon

Because of the size of the diencephalon, there are many commissure dedicated to connecting various sectors of the body. Some of these connect externally and pass through the internal capsule. These are included in the corpus principia of this work. Others are found entirely within the individual volumetric structures of the thalamus. They frequently connect specific engines to what appear to be extensions of the TRN interweaving between parts of the

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[44]Nolte, J. (1999) Op. Cit. pp 393-395

[45]Mitrofanis, J. & Guillery, R. (1993) New views of the thalamic reticular nucleus in the adult and the developing brain *TINS*, vol. 16, no. 6, pp240-245

thalamus.

15.6.1.3.4 Visual and oculomotor pathways based on morphology and pharmacology

As noted earlier, Tasker, et. al. have described the morphological pathways to and from the thalamus, and the effects of their electrophysiological stimulation in some detail.

Asanuma has provided an insight into the pathways internal to the thalamus based primarily on staining and pharmacology[46].

15.6.1.4 Gross architecture (topology) of vision in the diencephalon

To appreciate the following material, it is important to recognize the fact that the higher levels of the cognitive and control system, primarily the anterior and parietal lobes of the cerebral hemispheres, do not employ signals that are visuotopic. They use higher level concepts in machine language that describe the "content" of the environment around the organism via a comprehensive saliency map. This is the operating mode suggested by the Schematics and Functional Diagrams of PART I of this chapter and confirmed in **Section 15.6.4**. In this context, a major role of (at least part of) the diencephalon and of the occipital lobe of the *neo*-cortex is to convert the visuotopic information they receive into spatially abstract machine language that can be used by the higher cognitive engines.

Operations analysis, including traffic analysis, and physiology, including electrophysiology, suggest a major role for the thalamus in processing the sensory signals of the visual system of man. These studies do not require, or even suggest, any retinotopic mapping related to these higher level functions. More recent electrophysiological studies have reported multiple retinotopic maps within the thalamus, and more importantly within the thalamic reticular nucleus. However, their spatial fidelity varies widely. It is proposed here that most of these maps are descriptions of the receptive field of specific engines rather than retinotopic. This situation suggests morphologically tracing of the relevant signal paths may be more difficult than for the paths related to the optical radiation related to the LGN and the so-called primary visual cortex.

Similar traffic analyses and electrophysiology have presented a different picture with respect to the mid brain. While the signals of the superior colliculus show a clear, but rough correlation, with the field of view of the visual system, it is not always clear whether this view is the instantaneous or total field of view. In fact, it frequently appears to be a part of the saliency map representing the entire exterior environment. The total field of view is only a fraction of this total environment. This interpretation would suggest the superior colliculus is prepared to produce instructions that cause the visual system to explore areas outside its instantaneous and total field of view. It would accomplish this by issuing simultaneous commands to the skeletal motor system to reorient both the eyes and the body as required.

Correlating and controlling the activities in the thalamus of the diencephalon, the superior colliculus of the mid brain and other elements of the precision optical system appear to be the responsibility of the thalamic reticular nucleus.

15.6.1.4.1 Visuotopic and abstract maps in the diencephalon EDIT

Many investigators have provided detailed information on the architecture and topology of the paleo-cortex as it relates to vision. The general case related to vision is shown in [**Figures 15.6.1-1** & **-4**]. A broader caricature related to all sensory and motor commissure from the thalamus appears in Carpenter & Sutin[47]. It is suggested here that each of their paths through the thalamus is actually through the control point (generally defined as the control compartment of the thalamic reticular nucleus) and is bidirectional.

Sherman & Guillery have devoted an entire chapter to the discussion of maps in the brain, with a specific focus on the maps of the diencephalon. They note the multiple maps found within various morphological elements of the thalamus (para. A-2). Their description of the fragmentary nature of the maps found at different locations within the thalamus is useful. Of particular interest in vision are the highly correlated retinotopic maps within the lateral geniculate nuclei. These relatively coarse maps are well correlated along perpendiculars passing through the multiple layers of these nuclei. Each layer corresponds to a luminance or chrominance plane of one eye. The LGN's have the responsibility of correlating these maps to form two composite binocular images that can be passed to the cerebral cortex. In performing this function, they automatically generate a vergence control signal that is passed to the precision optical system, possibly by way of the thalamic reticular nucleus, to aid in creation of the appropriate

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[46]Asamuma, C. (1997) Distribution of neuromodulatory inputs in the reticular and dorsal thalamic nuclei. *In* Steriade. M. Jones, E. & McCormick, D. Thalamus, NY: Elsevier, Chapter 3.

[47]Carpenter, M. & Sutin, J. (1983) Op. Cit. pg 487

oculomotor commands. There is a similar set of higher precision foveolotopic maps within the diencephalon. These also have the requirement of merging the signals received from each foveola into a composite image. As an auxiliary function, they appear to generate a precision vergence signal that can be forwarded to the POS. It appears that this high precision map is formed in a local portion of the thalamic reticular nucleus found next to and possibly overlaying the LGN's. It is important to note that these correlation tasks are much more important than the mere relaying of signals to the cerebral cortex.

The evidence for multiple maps in the diencephalon has been accumulating rapidly in recent years. There are more reported maps than recognized purposes for them. Some maps may be mirror images of similar nearby maps. This feature suggests they may be arranged to reduce the signal processing (manipulation of the data) between nearby maps. Lacking a "little green man," there is no significance to forward or reverse orientation (or top or bottom orientation). Orientation is only a matter of computational convenience.

Sherman & Guillery initially review some maps found in cats that are considered abnormal, primarily because we do not understand the reason for their layout (para. E). They then move to the more interesting and important maps of the thalamic reticular nucleus, TRN (para. F). The layout of the data in the TRN also appears awkward initially. However, it is proposed that the layout is ideal for the task at hand.

There is some controversy in the literature concerning the passage of various commissure through the TRN. Sherman & Guillery follow Nolte in stating that; the thalamocortical and corticothalamic neurons passing through the TRN give off collateral branches that terminate in the TRN, but the neurons themselves do not terminate. However, those performing retrograde stains have drawn conflicting conclusions. Some say the dyes do not pass through the TRN. It is therefore concluded that all the neurons terminate in the TRN. The results of Crabtree clearly show the dyes injected into the cortex of rabbit passing to both the TRN and other nuclei of the thalamus[48]. He obtained similar results for the cat[49]. This data appears to confirm the position of Sherman & Guillery, at least regarding the majority of the TRN.

The TRN is divided into at least two functionally different compartments. One compartment appears to be involved in the very high level correlation of vector information from a variety of sensory channels. This results in the generation of new high level vectors. The other compartment, located adjacent to and apparently overlaying the LGN's, appears to be more concerned with the correlation of the signals obtained from the imagery projected on the foveola. This structure is called the perigeniculate nucleus, or PGN (and has been discussed previously within the context of a pretectum).

Sherman & Guillery also note three points concerning the maps in the TRN (pp 224-226). While their points are valid, this work will place a different interpretation on those points. First, they speak of the accuracy of the maps and the relatively large receptive field associated with the individual neurons in (an unspecified area of) the TRN. Second, they speak of "the surprising orientation of the reticular maps and the relationship of these to the complex crossing in the reticular nucleus." Third, they note that "within any one sector of the TRN, . . . one sees a representation of several thalamic nuclei or nuclear subdivision and also of several cortical areas concerned with the modality to which that sector is primarily dedicated." These are not the features of a device designed to accurately relay signals representing precise imagery. They are the features of a correlation or translation device, leading to the creation of a saliency map in machine language (as opposed to retinotopic coordinates). One of their final lines suggests "This arrangement of axons can now be related to the convergence, divergence, and reversal of maps between several cortical areas and thalamic nuclei . . . that we noted earlier." It is suggested that these are inappropriate nouns for describing signals in machine language space. A more appropriate set might relate to the processing of vectorized information. Examples might be verbs including merge, subdivide, compare, store and recall--etc.

Finally, the "maps" of the pulvinar and other major nuclei of the thalamus should be considered. These structures are three dimensional and do not show the clear topographic or topological organization of those elements discussed above. The neurons of these bodies are generally known, based on single probe measurements of selected axons, to be excitable by a large number of individual photoreceptors of the retina. The key fact is that the same photoreceptor in the retina can excite a vast number of neurons within a specific nucleus. However, only a selected set of photoreceptors in the retina can excite a specific sensing neuron in a specific nucleus. This is the key concept

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[48]Crabtree, J. (1992a) The somatotopic organization within the rabbit's thalamic reticular nucleus. *Eur. J. Neourosci*. vol. 4, pp 1343-1351, fig 6

[49]Crabtree, J. (1992b) The somatotopic organization within the cat's thalamic reticular nucleus. *Eur. J. Neourosci*. vol. 4, pp 1352, 1361

in the operation of these bodies, and the key concept in the operation of any programmed read-only memory, PROM.

15.6.1.4.2 Specific orientation of various maps within the diencephalon

There is very little precise data on the maps reported within the diencephalon. This makes differentiation between the types and purposes of the maps difficult. Crabtree has provided the best available data on maps within the somatosensory supervisory compartment of the TRN. However, these do not appear to apply to the PGN or the control compartment of the TRN. A more detailed discussion of the compartments of the TRN is given in **Section 15.6.2.** Sanderson has written on the maps of the LGN. No definitive maps of the PGN or the pulvinar have appeared in the literature.

Figure 15.6.1-3 from Crabtree is one source of the proposal that the TRN is arranged in slabs that relate to other thalamic nuclei. Here, the abbreviations relate to the somatotopic responses of the hindlimb, forelimb, head and tongue. Based on his detailed results, the lines between these areas are only conceptual in the TRN and should not be taken too seriously. The zones are part of a continuum. Crabtree says the unlabeled area below the TG in the TRN stains differently and is called the inner small cell region.

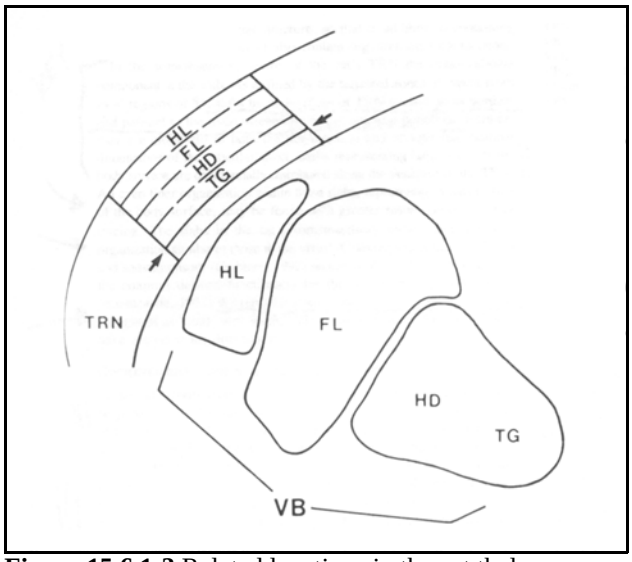

Figure 15.6.1-3 Related locations in the cat thalamus based on dye insertion in different cortical areas. Note the dashed lines within the TRN. See text. From Crabtree, 1992b.

Crabtree went further and provided the relative orientations of the retinotopic maps within each of the above somatotopic nuclei. **Figure 15.6.1-4** shows such a relationship for one thalamic nucleus. He notes that such slabs lie in the plane of the TRN parallel to its borders and parallel to the main orientation of the reticular dendrites. He also repeats in this paper, "like the geniculate columns these cortical input slabs cannot be thought of as 'units' because they should be continuously distributed without identifiable borders."

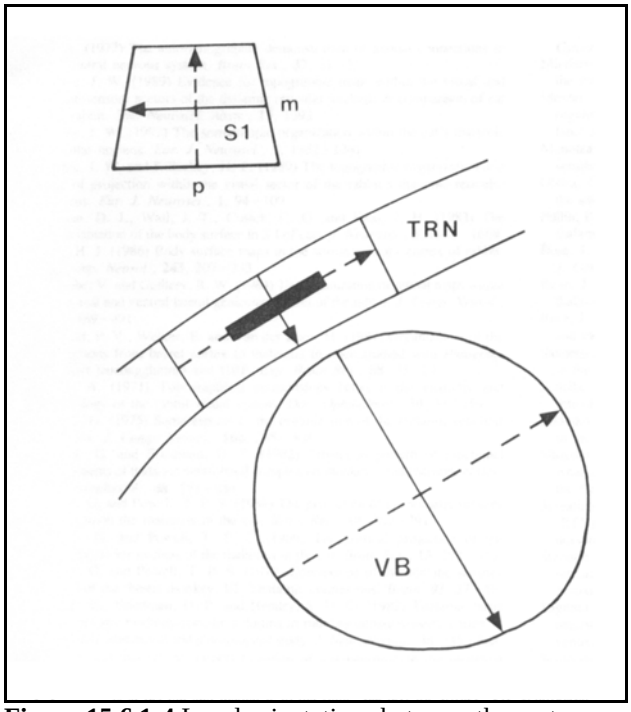

Figure 15.6.1-4 Local orientations between the cortex, TRN and one nuclei of the thalamus. The figure represents a horizontal plane through the thalamus. Rostral is at the top and medial is to the right. S1, somatosensory cortical area 1. VB, ventrobasal complex. m, medial. p, posterior. From Crabtree, 1992a.

This figure should be compared with his figure 10 in 1992b to emphasize these are only local orientations. The cerebrum is too highly folded to allow a fixed large scale orientation. In addition, there are geometric reversals related to different nuclei.

Crabtree says that "while the rostrocausdal dimensions of the slabs can vary in length, the dorsoventral dimensions are all approximately one millimeter in extent in the rabbit. Sanderson has provided some old but useful information concerning several species[50]. In both the rhesus and squirrel monkeys, he gives the cortical magnification factor for the central (foveal) part of the retina as 6mm/degree. For the cat, he gives a value of 1-2 mm/degree in the cortex and 0.6 mm/degree in the LGNd. In Sanderson's time, the LGN was thought to consist of only three layers. However, writing in the same year, he reflects on a claim by Guillery (1970) that it might consist of five layers, with the characteristics of the fifth being unusual[51]. None of these papers discusses the nature of the illumination used to stimulate the eyes of the subjects. The fifth (and probably sixth) layer would be associated with the violet-yellow Hering axis. Isolating these layers would be hard unless the color temperature of the light source was near 6500-7053 Kelvin.

In the second 1971 paper, Sanderson provides a full set of "Standard projection maps" of the LGN of the cat. He also provides a good discussion of the binocular properties of the cat based on these maps. The maps provide azimuth and elevation angles relative to the object space of the animal's eyes. A description of the retinotopic maps in object and retinal space was also provided. Sanderson, et. al. provided additional definitions concerning these coordinates[52]. He indicates the accuracy of his measurements is on the order of 0.9 degrees. His figures also show the serpentine nature of th TRN in some projections.

Sanderson says his maps confirm the earlier finding of Stone & Hansen (1966) that the Line of Fixation of the cat's eyes is not normally included in the retinotopic maps of the LGN. He shows it to be in the structure he labels the medial interlaminar nucleus, MIN, and states the projection there is a mirror image of the LGNd representation. He also claims there is an additional representation of the visual field within the PGN. Although a good discussion was presented, not enough material was presented to rationalize these facts further. Crabtree (1971b) also discusses the image reversals found between various maps in the thalamus of the cat. Since these maps are found in the feature

[50]Sanderson, K. (1971a) Visual field projection columns and magnification factors in the lateral geniculate nucleus of the cat. *Exp. Brain Res*. vol. 13, pp 159-177

[51]Sanderson, K. (1971b) The projection of the visual field to the lateral geniculate nuclei in the cat. *J. Comp. Neur*. Vol. 143, pp 101-117

[52]Sanderson, K. Bishop, P. & Darian-Smith, I. (1971) The properties of the binocular receptive fields of lateral geniculate neurons. *Exp. Brain Res*. vol. 13, pp 178-207

extraction engines of the brain, their occasional reversal should not be given too much weight. There is no need to recreate a true retinotopic image later. The reversals are more likely used to provide a simpler topological organization of the feature extraction circuitry.

15.6.1.5 Top level signaling architecture surrounding the thalamic reticular nucleus

15.6.1.5.1 Electrical signals to and from the thalamus

To begin this important area of study, **Figure 15.6.1-5** is offered as a generalized description of the visual system of man. While the terminology is slightly different, the signal flow is the same as that shown in the top-level schematic diagram and the top-level functional diagram of **Section 15.2.3**. It is also in general agreement with the caricatures of Robinson & Petersen[53]. While they show two distinct paths between the retinas and the diencephalon, they show the termination points rather nebulously, at the medial pulvinar and the inferior pulvinar. This work will show these paths (commissure) terminating at the LGN and PGN. Their paper was one of the first to explore the idea of a control point that determined the mode of visual spatial attention. While they mention the TRN, they concentrate on the role of the pulvinar in controlling attention.

In this interpretation, there are three functional pairs of elements, and one stand-alone element. Each operates in a distinct operational sector of vision and occupies an anatomically definable region of the brain. The superior colliculus and the cerebellum operate primarily in the oculomotor and skeletal motor regimes. The PGN and the pulvinar operate primarily in the regime of the central portion of the retinotopic map associated with the foveola. The striate and prestriate regions of the occipital lobe operate primarily in the regime associated with the peripheral retinotopic map. The LGN is concerned primarily with deriving stereopsis and alarm signals while merging the images forwarded to the striate cortex. All of the information processed by these operating elements is evaluated and switched by the TRN of the thalamus (based on instructions and ground rules provided by the anterior lobe). As part of the evaluation and switching, signals from other modalities and other regions of the thalamus are also reached. One result of this processing is the formulation of a comprehensive saliency map.

In this interpretation, the TRN is the control point that determines not only the focus of visual attention (and also that of other modalities) but also the expression of emotion and the skeleto-motor activity of the body.

The dashed box highlights a problem in the terminology of the TRN. While one area, the perigeniculate nucleus (PGN) has been given a distinct name, the rest of the TRN has not been subdivided as clearly. Mitrofanis & Guillery have touched on this problem and described an additional area designated the perireticular nucleus[54]. They have also suggested other region-specific differences might be found. Their discussion, and the subsequent one by Mitrofanis[55], focuses on the dynamics of the morphogenesis of the perireticular region (variously described as a plexus or nucleus). There is a need to use stereotaxy to define many regions of the TRN, in association with individual modalities or individual signal paths where feasible.

A second problem involves the detailed nature of the signals shown passing through the TRN. The literature is conflicting in whether an individual neuron passes through the TRN without interruption (but with Nodes of Ranvier present) or whether there is a serial synapse within the TRN. The conflict may be resolvable on a regional basis. In either case, it appears that axonal collaterals are present that terminate within the TRN.

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[53]Robinson, D. & Petersen, S. (1992) The pulvinar and visual salience *TINS*, vol. 15, no. 4, pp 127-132

[54]Mitrofanis, J. & Guillery, R. (1993) New views of the thalamic reticular nucleus in the adult and the developing brain *TINS*, vol. 16, pp 240-245

[55]Mitrofanis, J. (1994) Development of the thalamic reticular nucleus in ferrets with special reference to the perigeniculate and perireticular cell groups *Euro. J. Neurosci*. vol. 6, pp 253-263

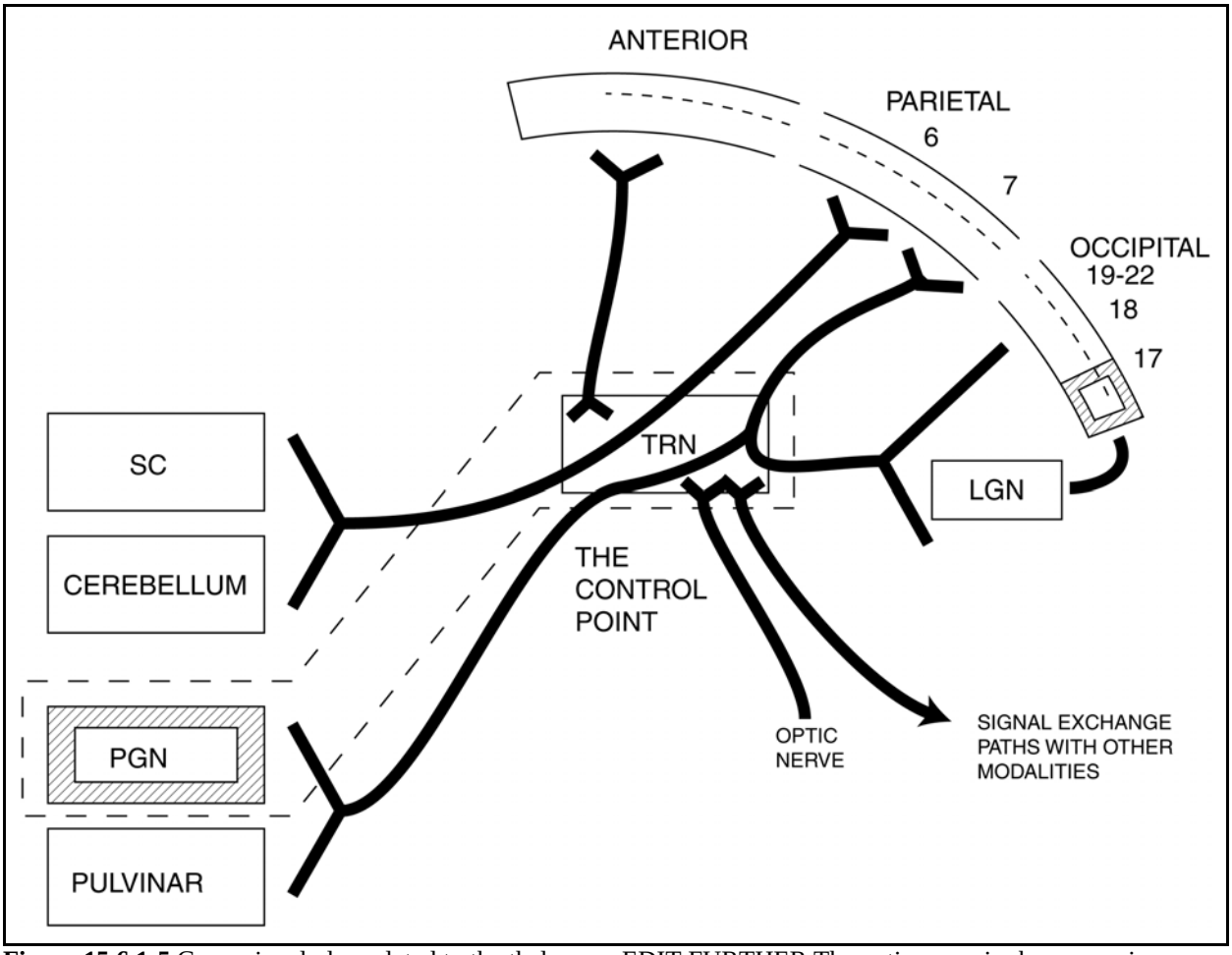

Figure 15.6.1-5 Gross signal plan related to the thalamus. EDIT FURTHER The optic nerve is shown passing through the TRN before proceeding to the PGN/pulvinar couple and the LGN on the way to the striate/prestriate couple. The fact that the surfaces of the PGN and the striate cortex are are patterned is indicated by hatching. The possibility that the LGN shows a finer patterning in its layers is indicated by stippling. Signals returning from the striate/prestriate couple probably do not pass through the LGN. The motor-oriented SC/cerebellum pair is shown for completeness and its role in eye movements.

Each of the signal paths shown between these operating pairs and the TRN are two-way commissure that carry both signal information and any required supervisory signals. In this configuration, the PGN and LGN both receive signals from their portions of the retina over the optic nerve.

Not shown are the similar signal paths, related to other sensory modalities, that also converge on the TRN. The TRN has a responsibility to merge all of this data into a comprehensive saliency map describing the environment of the organism at a given point in time. It is true the signals delivered to the LGN and PGN are largely retinotopic . However, it is the role of the striate/$V_{>2}$ couple and the PGN/pulvinar couple to extract the information from these maps and deliver abstract (non-retinotopic) information to the TRN. It is this abstract information that can be included in the overall saliency map of the organism. The resulting data is transmitted to area 7 of the cerebral cortex primarily via the so-called pulvinar pathway. Operational data is returned to the TRN primarily from area 6 of the parietal lobe. The data communicated between the anterior cortex and the TRN directly can be described as primarily supervisory in nature.

> As an example, it is proposed that supervisory signals direct from the anterior lobe may warn the TRN that command signals are coming to it via the pre-motor area of area 6. However, the detailed instructions will come via the signaling paths from area 6. These will then be routed to

the SC/Cerebellum for command implementation.

The thalamic reticular nucleus of the thalamus is seen to act as the critical element between the many activities of the brain. While the cognitive activities of the anterior lobe may be described as the highest level of cognitive activity, it is the TRN and other elements of the thalamus that keep everything operating as an entity.

While the above interpretation may seem strange to researchers in vision, who have always assumed that the signals delivered over the geniculo-calcerine commissure were predominantly one way, the brain research community has clearly shown that this is not so. Massive numbers of neural paths originate in the occipital lobe and terminate in the thalamus. As Mitrofanis & Guillery noted, "These thalamic relays themselves receive their heaviest innervation not from the periphery, but instead from axons that return from the cortex to the thalamus[56]. These pathways strongly suggest one point. The striate cortex is teamed with the non-striate portion of the occipital lobe in the reduction of the peripheral retinotopic signals just like the PGN/pulvinar is with respect to signals from the foveola. Research is currently under way, using fMRI and VEP techniques, that will establish how much of the information that reaches the striate cortex reaches the parietal lobe in a timely manner without passing back through the thalamus. There is another important question not documented in the current literature. Do the corticothalamic paths from the non-striate cortex exhibit an elongated path like that associated with Meyer's Loop? If they do, what is the purpose of such a feature?

The above interpretation of the various paths as fundamentally two-way, and also containing associated supervisory signal paths can be compared with the recent signaling framework of Sherman & Guillery. Within the above context, they define two types of thalamic relay, a first order (FO) and higher order (HO) relays. The first order relay accepts an afferent signal and passes on to the cerebral cortex a signal it has not seen before. The higher order relay is processing information that has been previously processed by at least one cerebral area (pg 249). Elsewhere, they define afferent signals as drivers and some types of previously processed information as modulators. They do not describe the character of the signals being processed by the HO relays. However, they do note three important points. First, Jones and his colleagues describe the connections of the reticular nucleus and the cortex and thalamus as not being mapped in a clearly defined topographic manner. Second, that mapping of two-dimensional signals into a three-dimensional volume offers many options. Third, Conley & Diamond showed that, in *Galago*, the visual reticular sector has two adjacent compartments, one mapped in terms of afferents from the LGN and the other apparently not mapped, with afferents from the pulvinar. This last point is extremely important and will be discussed further in the section on the TRN. It can be assumed that each pair described above process both mapped and unmapped signals. Unmapped signals are sometime labeled diffuse signals. They are more appropriately described as abstract signals. They will eventually become known as signals in machine language.

The model suggests that additional definition is needed concerning both the physical aspects of the thalamus, the nature of the signals received by the thalamus, and the nature of the processing performed by the thalamus. This involves a redefinition and broadening of the above terminology.

This work will replace and revise the definition of a driver pathway and modulator pathway. The generic descriptor, driver pathway, will be replaced with signal pathway. Pathways of this type will be limited to the transmission of signal information. The generic modulator pathway will be separated into both signal and supervisory pathways. The supervisory pathways will be limited to non-signal information. These definitions allow a greater formalization of the block diagrams of the thalamus. It will be shown that some signal information may be processed within a single engine to produce both signal information and supervisory information.

With the above definitions, the physical subdivisions of the thalamus can be more clearly differentiated and their functional role more clearly described. The caricature in Carpenter & Sutin, noted earlier, demonstrates the central role of the thalamus. Signal information arrives from virtually all of the sensory subsystems, and signals radiate from the thalamus to a wide variety of other cortical locations. Large sets of supervisory signals also arrive at and radiate from the thalamus. However, the caricature suffers many shortcomings. It does not suggest the actual shape of the thalamus. It does not segregate the pathways shown by modality and/or function. Nor does it recognize the most critical element of the thalamus, the thalamic reticular nucleus. These features are contained within **Figure 15.6.1-1**.

Such redefinition also aids in the interpretation of the mapped and unmapped signals described by Mitrofanis & Guillery.

15.6.1.5.2 The changing character of neural signals in the CNS

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[56]Mitrofanis, J. & Guillery, R. (1993) Op. Cit. pg 240

As the information originally contained in retinotopic maps is converted into more abstract information expressed in "machine language," it becomes more difficult empirically to track and interpret these signals. It is likely that the information will often be carried in word- serial, bit-parallel format such as used in a modern computer to communicate between the CPU and the peripherals (such as a printer). In this signal format, empirical exploration using a single electrical probe will generate negligible information about the operation of the system. To make significant progress, a different experimental methodology will be needed. The stage 3 ganglion cells associated with a given commissure (or portion of a commissure dedicated to a particular message) will need to be interrogated using a multichannel-input word analyzer as currently used to locate faults in circuit boards. Unfortunately, even isolating these channels will be difficult until crypto-analysis has succeeded in determining the format of the machine language used within the CNS.

15.6.1.5.3 Detailed nature of the electrical signals within the thalamus

Because of the gross difference in concepts between this work and the biochemical literature, no attempt will be made to correlate the two. For background, Chapters 6, 8 and 10 of Steriade, et. al. vol. 2 provide considerable data regarding phasic signaling to, from, and within the thalamus. However, these chapters do not recognize tonic signal processing as the dominant mode in the engines of the thalamus.

In addition, one should consider the waveforms shown in Nolte (pg 399 in 2001). While he defines two different signaling modes, the tonic and burst (phasic) mode. He illustrates but does not elaborate on the two different styles within the burst mode. Both were generated artificially for purposes of illustration. As will be shown below, each single action potential can represent a single bit in a parallel vector containing many bits. Thus, a series of action potentials is merely an artifact of the underlying signaling. Each action potential in a naturally occurring burst may relate to an entirely different vector.

In addition, crosstalk between adjacent neural channels can distort the measured signal significantly.

15.6.2 The key role of the thalamic reticular nucleus

The thalamic reticular nucleus, TRN, is placed in a powerful position between the sensory facilities, the internal elements of the thalamus, and all other elements of the cortex. However, the thalamic reticular nucleus hardly appears in the vision literature before 1980. Since then, it has been explored quite extensively and its role described by several investigators. Obtaining a comprehensive view of the TRN remains difficult because of the different perspectives of the various investigators. Some investigators have defined paradoxes based on such perspectives[57]. They noted differences in PGN activity related to the state of wakefulness that they could not interpret within the scope of their study. Without controlling or monitoring all of the relevant supervisory and command inputs, they conclude that "The responses of perigeniculate cells are notoriously variable." Others have used more general terms than wanted for similar reasons.

Previous investigations have been largely limited to staining, radioisotope tagging and other morphological tracing procedures. Most have not been sufficiently comprehensive to describe the complete role of the TRN. There is a great need for a broader framework in which to consider the functions of the TRN. This framework must define the signaling architecture of the system. With an available signaling architecture, it becomes possible to explore the individual electrolytic circuits of the body. This in turn leads to an appreciation of why much of the TRN is reticulated (its surface exhibits a woven appearance). In presenting this broader perspective, reinterpreting the words of many prior investigators in this larger context is necessary. It is hoped these reinterpretations will be received in the interest of moving our knowledge of the entire subject forward.

The fact that the thalamic reticular nucleus and other parts of the diencephalon are significantly different in humans than in other higher primates is also important. It is in the TRN that significant differentiation occurs. However, it also extends to differences in the *neo*-cortex[58]. This complicates the research role based on the use of surrogates. Fortunately, the arrival of new imaging techniques may alleviate this problem and provide more direct analyses of human cortical performance.

This section will present significant new material that establishes the critical importance of this little known morphological structure. It will show that the TRN represents a major switching point in the neural system. For

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[57]Murphy, P et. al. (1994) Brain-stem modulation of the response properties of cells in the cat's perigeniculate nucleus. *Visual Neurosci*. vol. 11, pp 781-791

[58]Tootell, R. & Hadjikhani, N. (2001) Op. Cit. Pg 298

purposes of this work, **it is THE control point of the total and complete neural system**. It not only controls what is presented to the higher cognitive centers of the brain but it controls the alarm and analytical modes of the visual process. It also controls, if not participates in, the unique capability of humans to read. It also controls the response of the oculomotor and skeletomotor systems, including the expression of emotion.

Another role that appears to be the responsibility of the switching portion of the TRN is the blanking (or blockage) of sensory inputs arriving from the retina during saccades. Such blanking is needed to prevent the introduction of extraneous signals, during the saccades, that would reduce the signal to noise performance of the system. See **Section 15.3.5.1**. Robinson & Petersen note that about 30% of the neurons of the pulvinar show a response to eye movements, even when the eyes are exposed to total darkness. This appears to be confirmation of a blanking function, whether controlled by the TRN or not.

15.6.2.1 Background and terminology

To understand the operation of the TRN, it is necessary to refine the terminology. The current terminology has evolved primarily from morphology and physiology. Differentiating between signals detected in the higher centers of the brain that are visuotopically mapped from those that are not is important. Many of these abstract signals exhibit a large receptive field relative to the retina as opposed to a high definition map. As an example, V2, the prestriate area of the occipital lobe has historically been considered visuotopically mapped. However, as Lozsadi has pointed out, this area consists of 'multiple minuscule maps' or more appropriately multiple small engines with large receptive fields. The concept of centrifugal and centripetal signals also begins to fail when discussing the higher centers. Many signals are passed between various engines of the cortex that cannot be described as afferent or efferent. Therefore, the terms centrifugal and centripetal, and also orthodromic and antidromic, can only be used to describe local conditions.

Several authors have spoken concerning the predominantly, or totally, GABAergic nature of the neurons of the TRN. These statements should not be relied upon and are largely irrelevant (as noted in **Section 15.1.2.3.7**).

Mitrofanis & Guillery (93 conclusions) have discussed the morphogenesis of the TRN in their concluding remarks. They have noted the developmental role of the TRN in defining the basic signaling paths that become significant commissure at a later stage. They have also noted the complex role of the TRN in the mature organism, suggesting that the TRN is the "mediator of selective attention" and equally important "are thought to relate reticular activity to levels of arousal." The current discussion on this point in the literature is being obscured by the poor differentiation between the putative visuotopic mapping and receptive fields of specific engines in the TRN. It appears that the role of the TRN with respect to attention is quite separate from its role with respect to arousal and emotion. It appears the TRN plays a major role in determining the priority with which various sensory inputs are processed. In this way, it controls the sensory signals presented to the higher cortical centers and thereby controls what is described as the attention of the organism. After reviewing other materials related to the limbic system, it appears a better description of the relation of the TRN to emotions can be defined. Based on the switching function of the TRN, it is proposed that the TRN plays an important part in controlling both the observable level of arousal and the display of emotions. It probably does not play a role in establishing these observables.

15.6.2.1.1 The morphology of the thalamic reticular nucleus

Few images of the thalamic reticular nucleus (TRN) as an entity are found in the literature. This is undoubtedly due to the physical complexity of the shape of the TRN as a covering to the underlying thalamus. This section will quote a variety of investigators. The reader is cautioned that they do not always clearly define what area of the TRN they are addressing. The reader is also cautioned that the higher primates differ significantly from the lower species in the area of the TRN (and the pulvinar).

It is proposed that the TRN needs to be subdivided into a group of compartments, each exhibiting a distinct function. These compartments should probably be aligned with the modalities they relate to, and its overall control function. Three compartments are critically important to the visual system. They are the central control compartment, the supervisory compartment related to the performance of the LGN and the PGN, and the PGN (Perigeniculate nucleus) as a compartment.

Figure 15.6.2-1 reproduces a micrograph of a macaque monkey from Hendry, et. al. It clearly shows the TRN as a thin shell wrapped around the VPL and VLA regions. Steriade, et. al. (page 76) have reproduced additional pictures of the anterior monkey thalamus provided by Jones. Figure 2.17 in Steriade, et. al., also from Jones, shows the location and filamentary structure of the TRN in the rat. Based on Steriade, et. al.(page 114), "it is a relatively thin sheet that surrounds the anterior, lateral and to some extent ventral surfaces of the dorsal thalamus, separated by the external medullary lamina." This image is not entirely representative of humans and other carnivore who are known to have a much larger pulvinar than in the monkey. In the descriptions for these species, the TRN extends

posteriorly to enclose much of the pulvinar and approach the two LGN's. Near the LGN's, the TRN changes physical character. This area (compartment) has been labeled the perigeniculate (PG) or perigeniculate nucleus (PGN). This change in character appears in consonance with this work. Here, the PGN corresponds to a multi-dimensional correlator associated with the foveola. Many thalmocortical and corticothalamic commissure pass through the TRN at multiple locations. Steriade, et. al. suggest the multiple holes in its surface give the nucleus its name. However, this may be an inappropriate attribution. Sherman and others relate the word reticular to the woven appearance of the TRN surface. Some authors even suggest the commissure are grouped into a single sheet where they pass through the TRN. In each of these areas, a picture is worth a thousand words.

Steriade reviews the attempt of Macchi, et. al[59]. to described the relevant commissure regarding their ultimate destination and degree of concentration at the destination. It is a useful effort but clearly preliminary. They do note differences between those commissure emanating from the geniculate bodies and the pulvinar. They describe Class I connections as consisting of "a major thalamic afferent pathway and projecting densely upon an anatomically and functionally homogeneous cortical field, . ." Their Class II connections, including the pulvinar, "receive multiple sets of afferent pathways and project densely upon one cortical area and less densely upon other, functionally related areas."

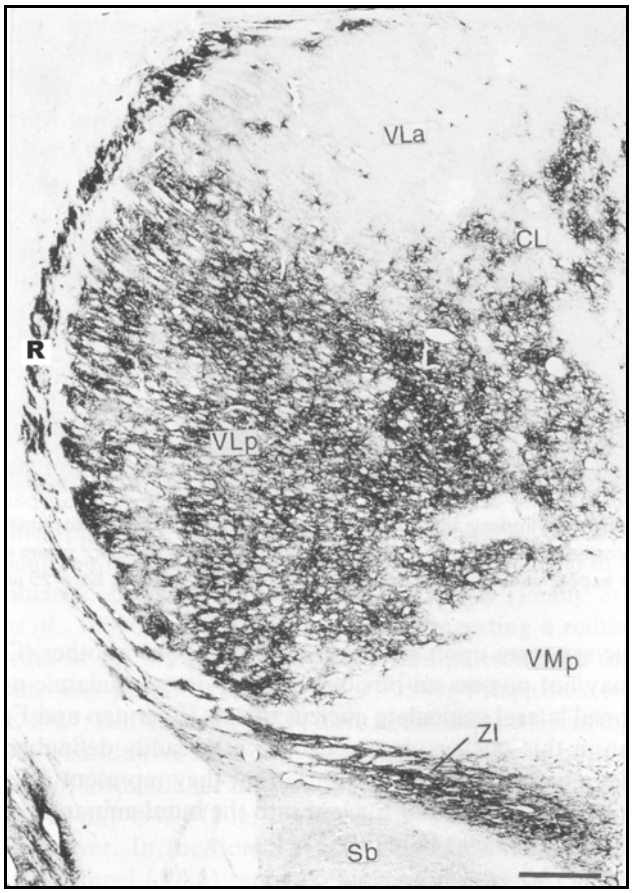

Figure 15.6.2-1 Frontal section through the thalamus of a macaque monkey, showing the TRN. This shows the extent of the reticular nucleus (R) and its overlap with the zona incerta (ZI). Scale bar = 500 microns. From Hendry, et. al. 1988.

The recent work of Sherman & Guillery has shed considerable light on the thalamic reticular nucleus as a unique structure clearly positioned to act as a gatekeeper within the thalamus[60]. However, it appears also to support a range of other functional capabilities. Its intriguing aspects are primarily two. It is a node, through which nearly every neural path between the nuclei of the thalamus and their ultimate connections in the cerebrum must pass. Further detailed analysis is necessary to decide if this statement includes the optic radiation. Second, its unusual lattice like structure is highly suggestive of a switching matrix. In the 1960's, a telephone system designer would see this structure as analogous to a crossbar switch. In the 1970's, the same designer would look at the structure as a matrix switch (generally employing a diode or transistor at each cross-point of the matrix). Two of the features of such a matrix are particularly interesting. Such a switch can act as a highly versatile path-switching network. It can handle many independent paths through the switch simultaneously and it employs only a few switching components per path. Secondly, by properly configuring the same switch, it can act as a two-dimensional correlator. Multiple outputs can be obtained simultaneously based on multiple inputs and the state of the internal cross-points. The above mechanical switches were usually made in sizes of 100 x 100 (10,000 inputs) and the electronic matrices are currently widely used in 1000 x 1000 (10^6 inputs) configurations. Either of these configurations is compatible with the nominal 23,000 inputs provided by the foveola.

An even closer analogy exists between the rough wool quilt-like appearance of the TRN at a small scale and the special memories used in manned space flight to avoid susceptibility to radiation damage. A woven magnetic core

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[59]Macchi, G. et. al. (1996) Trends in the anatomical organization and functional significance of the mammalian thalamus. *Italian. J. Neuro. Sci.* vol. 17, pp 105-129

[60]Sherman, S. & Guillery, R. (2001) Op. Cit. pp 211-225

memory is used in spaceflight for stability in a radiation environment. With a little defocus, telling the difference between pictures of the two is difficult. The woven core memory is available in two versions. One version is a simple switching matrix as described above. If an additional set of control wires is woven through the memory, it becomes a very efficient associative memory (or correlation device). Goodyear Aerospace manufactured these associative (parallel) memories in the 1960's before the speed of serial computers increased to the point that their advantage was lost.

Steriade, et. al. have pointed out the proximity of part of the thalamic reticular nucleus to the lateral geniculate nuclei. In some species, this portion of the TRN has been labeled the perigeniculate nucleus (PG or PGN)[61].

15.6.2.1.2 Electrophysiological framework in the current literature

The information appearing in the literature concerning the TRN is sparse. This area is clearly at the leading edge of current investigations into the operation of both the neural and visual systems. Sherman & Guillery have provided the latest comprehensive work on the TRN. It is found in Chapters 3, 5 & 7 of their 2001 text. Their summary and list of unresolved questions at the end of each chapter provide a framework that can be expanded upon here. By comparing their information with the model of this work, additional direction can be provided to the experimental investigator.

Sherman & Guillery highlight their conclusions;

1. Large parts of the thalamocortical pathways are known to have a topographically ordered projection but we lack information about the functional variable that is mapped.

2. Some of the modulatory (?, supervisory) pathways are also mapped, whereas others show no topographic organization.

3.Each major modality is represented by several maps. These maps frequently exhibit varying degrees of topographic order and are often mirror reversals.

While they clearly recognize non-retinotopic (non-visuotopic) maps are present, their constrained terminology makes it difficult to expand their baseline. This Chapter will expand on their terminology and make a variety of proposals concerning the operation of the TRN within the visual context. It will then present a set of more sophisticated models of the overall visual system.

Sherman & Guillery note (pg 223) the variability in degree of mapping associated with different modalities and the details of corticoreticular and thalamoreticular pathways in the cat. They conclude “This is an area where details of connectivity are seriously in need of attention, although it seems likely that a detailed account may have to wait.” They also conclude with three points that will be reordered and reinterpreted here.

(1) They note the considerable variability in the internal structure of the TRN.

(2) They address the range and granularity of the maps found within the TRN. This will be discussed further with respect to the retinotopic information, the physical dimensions of the TRN and the ultimate destinations of the output signals.

(3) They note the “surprising” orientation (and variation in orientation) of the reticular maps and the relationship of these to the complex crossings in the reticular nucleus. This variation in orientation is useful in defining the various compartments of the TRN.

Within any one compartment of the TRN, one sees a representation of several thalamic nuclei or nuclei subdivisions. One also sees connections to several cortical areas concerned with the modality to which that sector is primarily dedicated.

(4) A highlight of their discussion centers on the decreasing level of retinotopicity as signals approach the higher level centers of the cerebral cortex. In this context, areas 17 through 22 are lower levels of the cerebral cortex.

(5) Finally, the merging of signals from multiple modalities, and from multiple areas associated with each modality, is clearly related to the formation of the saliency map.

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[61]Steriade, M. Jones, E. & McCormick, D. (1997) Thalamus, vol. 1. NY: Elsevier pp 114-115

The portions of the TRN related to vision show significant variations in topography and topology. Study of the morphogenesis of the TRN has not provided a clear explanation of these differences. Its structure is clearly distinct from the LGN and it seems distinct from that of the pulvinar. (Cucchiaro & Guillery, 1984) Mitrofanis has provided some information on the morphogenesis of the TRN at the detailed level[62]. A more global evolution from the basic layers of the brainstem would be useful in learning the interrelationships between the TRN, the thalamus and the limbic system. Mitrofanis & Guillery have also provided data on the paths related directly to the TRN[63]. Lozsadi has provided more information focused on paths between the cerebrum and the TRN[64] as well as data related to the connections between the TRN and the anterior thalamic nuclei[65].

As noted by Sherman & Guillery, "The mapped relationships that are established within the TRN must be understood before the purpose of the commissure can be understood." Unfortunately, most of the tracing of commissure to date has been to and from the occipital lobe of the cerebral cortex. There is a need for more comprehensive tracing from the parietal lobe and regarding the optic nerve. The latter should be focused on the neural tracts from the foveola. There appears to be no information in this area.

15.6.2.1.3 Electrophysiological data in the current literature

Montero, Guillery & Woolsey have written on the retinotopic aspects of the TRN in rabbit[66]. However, they did not write in terms of a perigeniculate nucleus. It appears that their work was focused on the supervisory role of the TRN and not the correlation role of the PGN. They found disks within the TRN that were oriented parallel to the surface of the TRN. The paper is an early one and provides valuable background. However, it should not be relied upon for specific information related to the PGN. They do note the long neuritic spines associated with many areas of the TRN. Conley & Diamond[67] have written on the visual sector of the TRN and said it contained several compartments. They appear to have concentrated on what would be called the supervisory compartment in this work. Conley, et. al[68]. have written on the TRN more generally when discussing the auditory system. Both studies were with the prosimian bushbaby, *Galago*. The latter study provides a good understanding of the density of neurons within the TRN. The former study provides gross stereotaxic information on the TRN. Both papers contain a long list of abbreviations. These papers help place the material presented recently by Sherman & Guillery, using the cat as a model, in context[69]. None of these species should be considered representative of the TRN of humans. However, they may provide first order templates or points of reference. They can also be used to place the recent book by Sherman & Guillery[70] in perspective.

15.6.2.1.4 Initial comments on the topology of the thalamic reticular nucleus

As noted earlier, the TRN is far from homogenous in physical characteristics. This also seems true of its topology (which drives much of the topography).

Sherman & Guillery (2001) have gone the farthest in developing the structure of the thalamic reticular nucleus. After introducing the headings, "Multiple Maps in the thalamocortical pathways," they note the profusion of maps related to the visual field found in the thalamus (page 210). After discussing some "Abnormal Maps in the Visual Pathways," they arrive at "Maps in the Thalamic Reticular nucleus." They describe the thalamic reticular nucleus as "a relatively narrow sheet of cells wrapped around the rostral, lateral and dorsal aspects of the thalamus." At some

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[62]Mitrofanis, J. (1994) Development of the thalamic reticular nucleus in ferrets with special reference to the perigeniculate and perireticular cell groups *Euro. J. Neurosci*. vol. 6, pp 253-263

[63]Mitrofanis, J. & Guillery, R. (1993) Op. Cit.

[64]Lozsadi, D. Gonzalez-Soriano, J. & Guillery, R. (1996) The course and termination of corticothalamic fibres arising in the visual cortex of rat *Euro. J. Neurosci*. vol. 8, pp 2416-2427

[65]Lozsadi, D. (1995) Organization of connections between the thalamic reticular and the anterior thalamic nuclei in the rat *J. Comp. Neurology* vol. 358, pp 233-246

[66]Montero, V. Guillery, R. & Woolsey, C. (1977) Retinotopic organization within the thalamic reticular nucleus demonstrated by a double autoradiographic technique *Brain Res*. vol. 138, pp 407-421

[67]Conley, M. & Diamond, I. (1990) Organization of the visual sector of the thalamic reticular nucleus in *Galago*. *Euro. J. Neurosci*. vol. 2, no. 3, pp 211-226

[68]Conley, M. Kupersmith, A. & Diamond, I. (1991) The organization of projections from subdivisions of the auditory cortex and thalamus to the auditory sector of the thalamic reticular nucleus in *Galago*. *Euro. J. Neurosci*. vol. 3, pp 1089-1103

[69]Sherman, M. & Guillery, R. (1996) Op. Cit.

[70]Sherman, M. & Guillery, R. (2001) Op. Cit.

locations, this thin sheet is subdivided into individual layers, not unlike the LGN's. They did not clearly differentiate between the various compartments of the TRN when discussing its maps. As those authors suggest, this is an area worthy of much greater attention.

Sherman & Guillery open a brief discussion of the cable properties of neurons in the context of the thalamus. It is based on Rall and includes many archaic ideas. Their idea of a cable is not supported here for reasons discussed in **Section 10.3.4**.

15.6.2.2 Gross signaling architecture internal to the TRN

It is difficult to separate the topology of the TRN from the terminations of the associated commissure. It is the terminations, primarily of external commissure, that are the primary source of information concerning its topology.

15.6.2.2.1 The literature relate to signaling in the thalamic reticular nucleus

The TRN has been studied in several species. Ohara & Lieberman studied connections between it and the dorsal lateral geniculate nucleus in the albino rat[71]. Montero, et. al. have performed more detailed radiographic studies on rabbits by injecting radio nucleotide labeled amino acids (in bulk) into the eyes and brain[72]. Conley, et. al. performed a pair of extensive studies on both the audio and visual portions of the TRN in the bushbaby, *Galagos* [73,74]. They differentiated between the bulk of the TRN and the perigeniculate nucleus, PGN (that is more highly developed and functionally differentiated in humans). Jain, et. al. have provided recent data on the tree shrew, *Tupaia belangeri*[75]. Several correlations between species were presented but they were largely restricted to the LGN. Sherman & Guillery provided a major invited review of the TRN in 1996[76]. They used the LGN of the cat as their main example and included a comprehensive bibliography. However, they did not address the TRN or PGN in detail. This work will focus on the PGN as a critical component in man's ability to read and analyze fine detail.

Jones has provided Chapter 9 in Steriade, et. al. vol. 2, focusing on the topography of the human thalamus. The multiple micrographs provide a comprehensive view of the TRN (labeled R in the figures). In many figures, the TRN (R) is clearly associated with stage 3 projection neurons. In other figures, there is a structure labeled R that appears to be TRN-like but is forming an internal medullary lamina. No stage 3 projection neurons are recognizable between the TRN and the adjacent nuclei. While he deprecates the lack of consistent nomenclature in the field early on, he proceeds without detailing his nomenclature. Later, he provides a useful concordance in Table 9.1. In that table, R (or Rt) is defined as the reticulatum thalami. On the last page, an additional table of abbreviations gives R = Reticular nucleus.

Most of the data regarding the TRN obtained to date has been via invasive and post mortem techniques involving staining, etc. New findings can be expected shortly as fMRI, MRI and similar techniques come into play. As the field moves closer to the use of local electrophysiology, a major need will emerge to adopt more detailed procedures in the stereotaxy of the TRN. When a typical engine of a million neurons occupies an area of only a few square millimeters, and adjacent engines are spaced accordingly, it is necessary to precisely differentiate and define the areas of the thalamus. If some adjacent engines are retinotopic and others are not, crucial elements of understanding may hinge on the precision of the taxonomy.

At this time, the precision of the taxonomy remains limited. Although Mitrofanis & Guillery say that the signals in the TRN related to the PGN/pulvinar couple exhibit both mapped and unmapped portions, and that zones between regions of the TRN exhibit multi modality merging. If the above findings are correct, the architecture of the

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[71]Ohara, P. & Lieberman, A. (1981) Thalamic reticular nucleus: anatomical evidence that cortico-reticular axons establish monosynaptic contact with reticulo-geniculate projection cells. *Brain Res*. vol. 207, pp 153-156

[72]Montero, V Guillery, R. & Woolsey, C. (1977) Retinotopic organization with the thalamic reticular nucleus demonstrated by a double label autoradiographic technique. *Brain Res*. vol. 138, pp 407-421

[73]Conley, M. & Diamond, I. (1990) Organization of the visual sector of the thalamic reticular nucleus in *Galago*, *Euro. J. Neurosci*. vol. 2, no. 3, pp 211-226

[74]Conley, M. Kupersmith, A. & Diamond, I. (1991) The Organization of projections from subdivisions of the auditory cortex and thalamus to the auditory sector of the thalmic reticular nucleus in *Galago*. *Euro. J. Neurosci*. vol. 3, pp 1089-1103

[75]Jain, N. Preuss, T. & Kaas, J. (1994) Subdivisions of the visual system labeled with the Cat-301 antibody in tree shrew. *Visual Neurosci.* vol. 11, pp 731-741

[76]Sherman, M. & Guillery, R. (1996) Functional organization of thalamocortical relays. *J. Neurophysiol*. vol 96, no. 3, pp 1367-1395

thalamus would suggest similar paired (or joint) regions related to the LGN/striate cortex, the SC/cerebellum and other modalities.

Mitrofanis & Guillery have mused on the organizational change that occurs between the (sheet-like) cortex and the (volumetric) diencephalon. However, because of their conceptual signaling framework, they do not give equal weight to other organizational changes. Features such as Meyer's Loop, between the diencephalon and the occipital lobe, and the equally important signal path between the diencephalon and area 7 of the cortex, are not addressed. The broader definition of the signaling architecture of the brain would stress these organizational changes tend to occur in both legs of a large, bidirectional, commissure. As a result, there are multiple "maps," applying to a specific retinal feature, in both the cerebral hemispheres and the diencephalon.

Several authors have noted the unusual morphology of the neurons of the TRN. McCormick, et. al. provide references and note; "Neurons of the TRN exhibit elongated dendrites that take the form of the TRN, which over most of its length appears as a sheet of neurons surrounding much of the lateral aspects of the thalamus." This tangent nature of the neural structure with the surface of the TRN appears in many photographs of Jones, but it is dependent on the specific orientation of the slices studied. It is particularly obvious in some of his drawings from the camera lucida (figure 9.3). The lengths and locations of commissure are also clear in these drawings. Steriade, et. al. (vol. I, pg 216-224) have noted two particular properties of the neurons of the TRN. First, they noted the large size, 25-50 micron diameter soma, of many of the neurons. Second, they noted the "long, smooth and relatively little-branched dendrites emerging from the poles of the soma; occasional spine-like protrusions appear on the dendrites and soma." Montero, et. al. also noted "the reticular map shows an elongation in the dorsoventral axis, which corresponds to the orientation of dendritic arbors within the nucleus." When discussing the retinotopic maps of the TRN, they also noted "it appears that the dendritic fields may relate to specific, limited parts of the visual field representation."

McCormick, et. al. also illustrate long axons with multiple collateral pedicles spaced along their length (from Scheibel & Scheibel, 1966).

The phasic neurons of both the TRN and its component, the PGN (see next paragraph), exhibit what McCormick, et. al. describe as both rhythmic burst firing and single spike activity (as well as no activity between these two forms.

These are not the properties of neurons used to accumulate (converge) sensory signals, they are the properties of neurons used in multi-state switching, multi-dimensional correlators and PROM circuits. The fact that adjacent parts of the thalamic reticular nucleus, relating to the paired PGN/pulvinar, are mapped and unmapped goes a long way toward confirming that this region is acting as a PROM. Such a PROM can extract "machine language" interps from the retinotopic input to the couple. The phasic operation of the neurons associated with this couple is also suggestive of the outputs from highly complex Boolean algebra calculations. The pulse-to-pulse interval is indicative of the signal processing interval within the circuitry. The nature of the overall signal train suggests that each action potential in the non-mapped output is one element in a multi-bit parallel signal (vector). McCormick, et. al. offer several comments regarding the nature of these signal trains during sleep and wakefulness.

Montero, et. al. provided an early investigation into the topology of the TRN using rabbits[77].

Sherman & Guillery have provided the most relevant top level description of the signaling architecture of the TRN of the cat[78]. After noting that the TRN is, strictly speaking, a morphogenic part of the ventral thalamus, they say the TRN;

1. receives collaterals from both thalamocortical and corticothalamic neurons passing through the TRN, and

2. sends no axons of its own (from the lateral TRN) to the cortex,

3. sends axons to the thalamus.

They also make the critically important observation that any population of analog neurons in an engine would be very difficult to identify based on currently used techniques (pg 1375). This work will develop the fact that many

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[77]Montero, V. Guillery, R. & Woolsey, C. (1977) Retinotopic organization within the thalamic reticular nucleus demonstrated by a double label autoradiographic technique *Brain Res*. vol. 138, pp 407-421

[78]Sherman, M. & Guillery, R. (1996) Op. Cit. pg 1374

neurons within the TRN operate in the analog mode and their role has not been adequately explored. It will also note that Sherman & Guillery limited their paper to the lateral portions of the TRN, which accounts for the parenthetic expression added to item #2. They did note "the midline and intralaminar groups of thalamic nuclei . . . are probably organized differently than the rest." Based on this study, a fourth item is added;

4. sends and receives supervisory signals to all regions (both old and *neo*-) of the cortex.

15.6.2.2.2 Proposed architecture of the TRN

Figure 15.6.2-2 illustrates the proposed complex relationships involving the TRN in the mature organism. This figure expands on a figure in Lozsadi[79] and is similar to figures in Mitrofanis & Guillery (93, fg 1 & 4). In the literature, vision is frequently associated with the dorsal and caudal portion of the TRN. However, the LGN and PGN are located more ventrally. The TRN itself can be divided into at least three distinct physiological regions;

1. Areas describable as supporting the switching (and/or combining) of abstract signals from multiple sensory inputs.

2. Areas performing a two-dimensional correlation function, specifically the perigeniculate nucleus, PGN, in the visual regime.

3. Areas involved in the supervision of the processes occurring in other nuclei of the old brain and lobes of the *neo*-cortex.

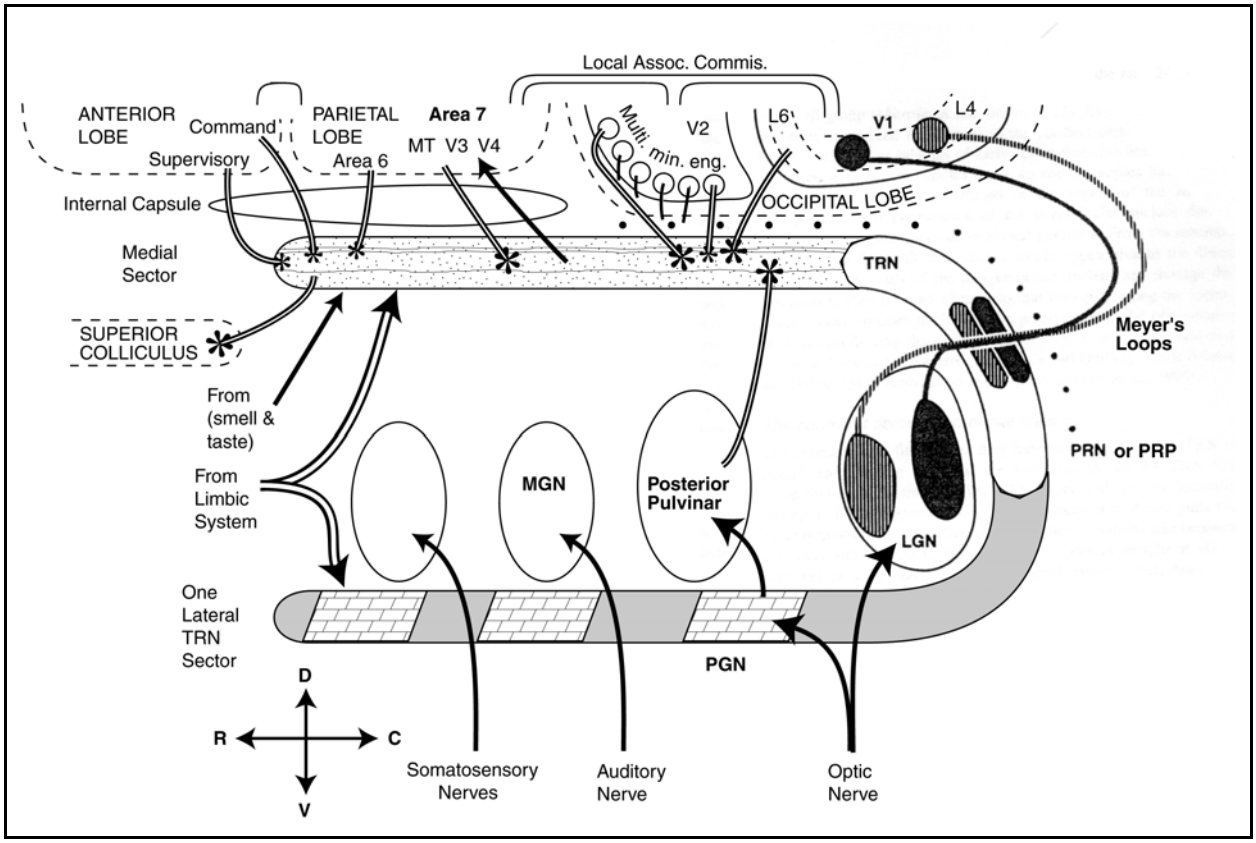

Figure 15.6.2-2 The functional role of the thalamic reticular nucleus. The U-shaped TRN is shown in three sections. The lower section is focused on processing sensory inputs. It includes the perigeniculate nucleus processing 2-dimensional data from the foveola. The right section is concerned with supervising centrifugal signals from the TRN. The top section is concerned with selecting and switching signals based on alarm mode inputs and previous experience. Solid paths are spatially oriented sensory inputs. Paths with white core are abstract signals.

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[79]Lozsadi, D. Gonzalez-Soriano, J. & Guillery, R. (1996) The course and termination of corticothalamic fibres arising in the visual cortex of the rat E. Jour. Neurosci. vol. 8, pp 2416-2427, fig 11

These three areas are highlighted in the figure by different background patterns. The two lateral TRN sectors perform several poorly documented functions. The most important with respect to vision is the two-dimensional correlation of the imagery from the foveola in the perigeniculate nucleus, PGN. The supervisory function is highlighted on the right. This compartment is known to contain "slabs" showing a topological resemblance to similar areas in the thalamus and in the *neo*-cortex. However, it is also known to contain areas that appear to be comparing signals from adjacent slabs related to different sensory modalities.

The solid signal paths in the figure represent afferent signals. The signals between the LGN and the neo-cortex represent signals from two areas representing equal elevations above the horizontal meridian in object space. The signal paths with a white core represent efferent signals.

Mitrofanis & Guillery have noted several key facts. "All of the axons that pass either way between the cortex and the thalamus must go through the thalamic reticular nucleus, and many of them, possibly all, give off collateral, excitatory branches that innervate the reticular nucleus." Further, "These thalamic relays themselves receive their heaviest innervation not from the periphery, but instead from axons that return from the cortex to the thalamus." Lozsadi, et. al. went further and noted that the neural paths to and from the occipital lobe do not pass through the same area of the TRN[80]. The striate portion receives signals from the laterally symmetrical parts of the LGN via the lateral (outer) two-thirds of the visual sector of the TRN. The prestriate portion returns signals to the medial third of the TRN. These comments were consistent with earlier remarks by Lozsadi that the TRN was not heterogeneous in rats[81,82]. The Lozsadi papers provide other references related to the interface of the TRN to the limbic, somatosensory and motor subsystems. These papers provide a wide range of specific features of different regions of the TRN. Most of them note the long linear neurites and axons of specific classes of neurons, and the general size and spacing of the various engines found within the TRN. They also note the more abstract (diffuse) nature of the signals returning to the TRN from the *neo*-cortex.

This work will generally follow the terminology used in the above papers, by Jones[83].

A major function of the TRN is highlighted by the medial TRN compartment. This compartment appears to collect abstract signals from a variety of sources, both internal to the thalamus and from other sources. It processes these signals in two distinctly different ways. It combines many abstract signals into more complex abstract signals associated with the saliency map. It appears to direct these abstract signals to other areas, primarily in the neo-cortex. Alternately, it accepts abstract command signals from the higher cortical centers (shown at upper left) and directs them to the appropriate part of the superior colliculus. There, they are processed further into specific oculomotor and skeletomotor commands. Jones, et. al. have described this switching and consolidation activity of the medial compartment as a 'global' function and described the connections between this compartment of the TRN "and the neo-cortex and thalamus as **not** being mapped in a clearly defined topographical manner." Lozsadi also discusses the multiple minute maps in the prestriate cortex. Based on the assumption these are visuotopically mapped instead of reflecting a visuotopic receptive field, he claims their neural paths back to the TRN terminate in topographically mapped order ('96, pg24-26). More recently, Tootell & Hadjikhani show the local sign within the area including dorsal V4 varies "seemingly randomly." Such action suggests this area is not visuotopically mapped but consists of many feature extraction engines exhibiting a variety of receptive fields related to object space.

The anterior lobe is shown directing supervisory commands to the medial portion of the TRN (extreme left). The associated action commands may be sent from the anterior lobe itself or they may be sent via the pre-motor complexes in area 6 of the parietal lobe. The name pre-motor is very appropriate because these abstract commands must be decoded into action commands within the superior colliculus.

Note that as the signals become more abstract, laterally symmetrical processing areas in the brain, to accommodate these signals, become redundant. Thus many identified processing areas of the parietal and anterior lobes are not paired and there is no reason for the TRN to maintain a visuotopic organization for abstract signals returning from feature extraction engines in the neo-cortex. Tootell & Hadjikhani have addressed this conceptual area when they

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[80]Lozsadi, D. Gonzalez-Soriano, J. & Guillery, R. (1996) Op. Cit. pg 2416

[81]Lozsadi, D. (1994) Organization of cortical afferents to the rostral, limbic sector of the rat thalamic reticular nucleus *J. Comp. Neurol*. vol. 341, pp 520-533

[82]Lozsadi, D. (1995) Organization of connections between the thalamic reticular and the anterior thalamic nuclei in the rat *J. Comp. Neurol*. vol. 358, pp 233-246

[83]Jones, E. (1985) Thalamus. NY: Plenum

ask "Where is 'Dorsal V4?'."[84] In the same paper, they note that the middle temporal area, MT, is not paired. They also noted that V4 was not topographically mapped in the monkey. Born & Tootell provide additional data concerning the columnar nature of the MT in owl monkeys[85].

Mitrofanis & Guillery provide a caricature showing the neurons of layer 6, apparently of area 17, returning to both the TRN and portion of the thalamus related to vision. The caricature is not detailed enough to discriminate between the switching and supervisory compartments of the TRN[86].

There is a significant interplay between the limbic system and the TRN as shown on the left. The limbic system, particularly the fornix, literally surrounds the diencephalon in many sectional views[87]. This would suggest it interconnects with the TRN and thalamus in many roles. Lozsadi has provided information of the rostral TRN associated with the limbic system and noted the unusual characteristics of the neural terminations[88]. His discussion seems to apply to both the switching and the correlation portions of the TRN. The discussion supports the heterogenic nature of the TRN with modality and location within the TRN. Multiple zones were found in some areas of the TRN that were essentially parallel to the surface of the TRN. However, the limbic terminations within individual zones formed "slabs" of neurons that were not parallel to the surface of the TRN. They note the more dorsal portions of the TRN exhibit slabs perpendicular to the surface of the TRN.

Besides addressing the gross signaling architecture of the vision related portions and the morphogenesis of the TRN, Mitrofanis has also addressed the architecture of the commissure adjacent to the TRN in ferrets[89]. He develops his discussion in terms of the commissure associated with the internal capsule, which he defines as the perireticular nucleus. This structure already has several names due to its complex shape. Here the name perireticular nucleus will be reserved for the area of the nucleus lateral to either lobe of the TRN. The commissure change direction significantly in this area. This designation is in general agreement with the 2-dimensional line drawings in figure 2 of Mitrofanis. Mitrofanis & Guillery address the commissure architecture showing it lateral to the TRN in both line drawings and electron-micrographs.

While the morphological community has addressed the interweaving of commissure at the lateral extremes of the diencephalon in terms of peri-reticular nuclei, PRN, the physiologist describes this area in terms of a peri-reticular plexiform layer, PRP. Mitrofanis & Guillery suggest, "it may be more useful to think of the perireticular cells as more of a sorting mechanism, separating fibres that have different properties." The various neural paths interweave to establish the most expedient paths to their terminating points. In the thalamocortical neurons, this interweaving also involves both the removal of time diversity (using Meyer's loops) and the computational anatomy leading to the visuotopic presentation at the striate cortex.

Steriade, et. al. have noted the direct connections between the basal forebrain and the thalamic reticular nucleus[90]. In addition, they note the widespread proliferation of the axons from the forebrain throughout the TRN. These connections are considered crucial to the supervisory and switching role of the TRN. They probably determine the operating mode of the TRN, and hence the organism.

The last paragraph of Lozsadi, et. al. is critical to understanding the operation of the LGN and the PGN. He notes a different in path between the foveal and peripheral neurons as they pass through the TRN. They note further, that "this may prove to be a true difference either between the pathways that represent central vision and those that represent peripheral vision, or between fibres that originate from area 17 and those from the prestriate cortex. Further experiments are needed to resolve this issue." This work sides with separate paths related to both of these options.

The geometric details of interweaving of the commissure are not critical to this discussion.

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[84]Tootell, R. & Hadjikhani, N. (2001) Where is 'Dorsal V4' in human visual cortex? Retinotopic, topographic and functional evidence *Cerebral Cortex* vol 11, pp 298-311

[85]Born, R. & Tootell, R. (1992) Segregation of global and local motion processing in primate middle temporal visual area *Nature*, vol. 357, pp 497-499

[86]Mitrofanis, J. & Guillery, R. (1993) Op. Cit. fig. 1

[87]Kretschmann, H. & Wienrich, W. (1998) Neurofunctional Systems. NY: Thieme pg. 90

[88]Lozsadi, D. (1994) Op. cit. pg 241-244

[89]Mitrofanis, J. (1994) Development of the thalamic reticular nucleus in ferrets. *E. Jour. Neurosci.* vol. 6, pp 253-256

[90]Steriade, M. Jones, E. & McCormick, D. (1997) Thalamus, vols 1 & 2. NY: Elsevier, Sect. 3.2.4.2

15.6.2.3 Supervisory & switching architecture & topology of the visual TRN

The detailed discussion of the TRN must recognize the differences between species in this area. The relative sizes and functions of the sections of the TRN change significantly among members of *Chordata*. The differentiation is particularly striking between the pro-simians and simians. Thus the papers of investigators must be carefully studied to determine the specific phylogenic context in which they apply.

Davenport provides a reference point in the phylogenic development process[91]. He notes that after the first week in chick embryos, the chiasm degenerates to a simple crossing. All remaining connections between the eyes and the brain are contralateral. His caricature presents a visual system that is quite simple. Because of the minimal binocular vision in chicks, there are no obvious lateral geniculate nuclei. The perigeniculate nuclei also seem absent in the chicken.

Ohara & Lieberman performed early studies, using horseradish peroxidase, to determine the nature of the neurons passing through and terminating in the TRN of the rat[92]. They did not study the neurons found entirely within the TRN. Later investigators have generally found that the neurons passing through the TRN do not have an in-line synapse within the TRN but many have collateral axons that terminate within the TRN. On the other hand, many other neurons, both from the neo-cortex and the thalamus, project axons terminating in the TRN.

The primary feature of the morphology of the TRN is due to the underlying nature of the neurons comprising the switching and correlation functions. These neurons have long neurites and/or axons, many of which are aligned with the surface of the TRN. These neural elements contribute to the woven appearance of the surface of the TRN from which it gets its name the reticular nucleus.

This section will review the architecture and topology of the supervisory and the switching compartments of the TRN. These characteristics are similar among all chordates. The architecture and topology of the correlation portions are uniquely well developed in human. The discussion of those characteristics will be found in **Section 15.6.3**.

15.6.2.3.1 Neural architecture & topology of the supervisory compartment of the visual TRN

Mitrofanis & Guillery have compared the visuotopic mapping within the supervisory compartment of the visual TRN and the dLGN[93].

15.6.2.3.2 Neural architecture & topology of the switching portion of the visual TRN

The switching portion of the TRN may be organized much like a crossbar telephone switch. With appropriate programming, any input circuit(s) can be delivered to any output circuit.

15.6.3 The crucial role of the PGN/pulvinar *couple* in humans and higher primates

This section will attempt to develop the relationships between the PGN and the pulvinar to provide a framework for defining the many types of output signals provided by these structures. The hypothesis will be that they work as a couple where the PGN is primarily a multidimensional correlator of visuotopic signals and the pulvinar converts the machine language features extracted by the PGN into higher level (and abstract) machine language signals. These signals can be distributed widely in the cortex. This distribution is in support of a variety of functions, including controlling the oculomotor and other skeleto-motor actions. The data base is not adequate to completely isolate the signal processing accomplished in the PGN from that accomplished in the pulvinar. This work will attempt to define experiments to isolate these processing steps further.

There is very little substantive material on the morphology of the PGN and the pulvinar related specifically to vision.

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[91]Davenport, R. Thies, E. & Nelson, P.. (1996) Cellular localization of guidance components in the establishment of retinotectal topography, *J Neuroscience,* 16(6): 2074-2085.

[92]Ohara, P. & Lieberman, A. (1981) Thalamic reticular nucleus: anatomical evidence that cortico-reticular axons establish monosynaptic contact. *Brain Res*. vol.207, pp 153-156

[93]Mitrofanis, J. & Guillery, R. (1993) Op. Cit. fig. 2

The majority of the information about the PGN is taken from sections cut perpendicular to the surface of the PGN. These were generally prepared for other purposes. Similarly, there is very little material that specifically describes the topography or neuroanatomy of the PGN.

The pulvinar was given that name (derived from the Latin for cushion) long ago. It is interesting to consider if it was given that name because of its softness. If so, was that softness required to insure adequate metabolic flow to the many neurons contained within its bulk? The pulvinar, along with many other structures of the thalamus, is not made up of highly folded thin layers like the cerebrum. The pulvinar is a volumetric. Its neurons form a thick three-dimensional mass. Annotating all of its individual regions has not yet been accomplished. It does contain an interior structure containing commissure and the lateral medial nucleus. Thus, it could easily accommodate a two-stage lookup configuration. It could also accommodate a single stage lookup table and a shift register.

The computational power associated with such a large number of closely associated neurons is mind boggling.

Steriade, et. al. (1997, vol. 1, pg 114) have suggested that the PGN is a feature of carnivores without rigorously defining that term. It appears to be too narrow when used in scientific literature. Humans are generally considered omnivores that descended from arboreal herbivores/insectivores. Many laboratory subjects currently used to study the PGN are herbivores or mixed herbivores/insectivores.

So & Shapley have studied the PGN, along with the LGN in the cat[94]. As they noted, "the perigeniculate neurons we encountered have very different receptive-field properties from LGN relay cells." One of their key observations involves the Y-cells of the cat. These cells are generally correlated with the magnocellular pathway in the primates at the conceptual level. The signals are actually spectral channel signals that have not been converted to luminance signals. In this respect they are not related to the signals in the magnocellular pathway. They found the signals delivered to the perigeniculate nucleus consisted primarily of Y-cells (monophasic luminance, or, as proposed here, raw spectral-channel signals). They recognized the awkwardness of this based on their previous conceptions and noted "However, we think that X LGN inputs onto the perigeniculate interneurons also must exist." They did not support their belief in this position and this work does not support it. The cat X-signals appear to be chrominance signals.

The TRN is noted for its multiple unique internal architectures. In a sense, the architecture of the PGN portion of the TRN is similar to the layered structure of the LGN. However, particularly in the PGN portion, the multi-layer structure does not form a spatial map parallel to the surface of the element and similar to the image projected on the retina. Individual zones of the PGN appear to relate to small areas of the retina (or foveola) but they are turned 90 degrees to the surface of the TRN. While this orientation destroys the spatial coherence of the information, it aids the formation of a multi-dimensional correlator. It reduces the length of the necessary control conduits, whether they be axonal or neuritical. Shosaku has presented one caricature of this structure from the somatosensory area of the cat[95].

Many authors have noted the extended structure of the axons and neurites of the TRN. Many dendrites are seen to extend across the entire cross-section of the TRN. They are also seen to bundle as if in a substructure relationship. Steriade, et. al. (page 120) note this substructure but doubt that it forms a spatially coherent retinotopic map. They note that some of the cells interrogated reflect a binocular field. They note; "Perhaps new physiological insights will help to indicate that the anatomical topography has some functional correlate, but at the moment it is difficult to see it other than a crude reflection of the topography inherent in the sensory pathways from periphery to cortex."

15.6.3.1 Visuotopic mapping relationships within the diencephalon complex

Figure 15.6.3-1 builds schematically on the previous figure. The TRN is shown surrounding, or incorporating several elements. Only the switching and correlation (PGN) compartments of the TRN are detailed. In this figure, the first order signal paths of Sherman & Guillery are shown by the heavy lines with white centers. The higher order signal paths are shown by thinner lines. Finally, the so-called last order, LO, signal paths are shown by a broad solid line. These are signal paths that extend directly to muscular tissue from the *paleo*-cortex. The PGN/pulvinar couple is shown surrounded by the TRN while the striate/$V_{>2}$ couple is shown within the occipital lobe of the *neo*-cortex. In the context of this figure, all signals from areas 18 &19 of the occipital lobe and areas 20-22 of the parietal lobe are

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[94]So, Y. & Shapley, R. (1981) Spatial tuning of cells in and around lateral geniculate nucleus of the cat: X and Y relay cells and perigeniculate interneurons. *J. Neurophysiol*. vol. 45, no. 1, pp 107-120

[95]Shosaku, A. (1985) A comparison of receptive field properties of vibrissa neurons between the rat thalamic reticular and ventro-basal nuclei, *Brain Res*. vol. 347, pp 36-40

abstract and proceed from those areas to areas 7a (the medial temporal, MT, and other areas)[96] via the TRN. Similarly, all volition commands emanate from area 7 and/or 6 (the pre-motor areas) and go via the TRN to the superior colliculus/cerebral couple for decoding and implementation.

The topological, and apparently the topographic, arrangement of some of these elements is shown on the left. The PGN physically overlays the LGN, and to a first approximation, its topology results in a visuotopic map that appears aligned with those of the LGN. However, on closer study, a variety of differences are seen.

While the three pairs of layers in the LGN are aligned to the two chrominance signals, P- & Q-, and the luminance signal, R, defined in this work, it is proposed the PGN is different. It is proposed that that the raw spectral signals, S-, M- & L-, are delivered to the PGN from the foveola. It is also proposed that these signals are treated as if they were achromatic, all being weighted equally, by the PGN. This methodology provides a higher spatial resolution to the PGN map compared to the magnocellular, or parvocellular, map of the LGN. It also appears this bundle of S-, M- & L-channel signals may be the signals typically described as Y-signals in cats.

It appears that the pairs of contralateral maps compared in the LGN are treated as if they were time coincident, and the time dispersal introduced by Reyem's loop produces a benefit. The stereopsis signal can be extracted based primarily on differential time delay between the contralateral images. It also appears that, once the two contralateral images are aligned within either LGN, they can be summed to produce a visuotopic map at the output of the LGN. The process involved can be compared with that of making a contact print. The topological image at the output of the LGN would be the same as that formed at the input. In this sense, the LGN can be considered a relay. As will be discussed below, the signal processing within the PGN is fundamentally different.

In the figure, the LGN is shown stippled, with short pairs of lines. This is to suggest it is performing a lower level of contralateral comparison than is performed in the correlators of the PGN and the striate cortex. These are shown as hatched. The spatial area of integration required within the LGN to extract the stereopsis signal is currently unknown, because the exact conformal transformation between object space and the LGN has not been developed. However, it appears, the LGN need integrate and sum over only a few pixels in LGN space to achieve its stereopsis and image merging functions.

The visuotopic map formed in the PGN is limited largely, if not totally, to the foveola. Thus, the total area of the map is limited to about one degree in object space. If covering about the same surface area as the maps in the LGN, the PGN map would exhibit a much higher *paleo*-cortical magnification factor. This would suggest that the PGN can extract a stereopsis error signal, angle ψ_2, with much more precision than that available from the LGN, angle ψ_1.

> It should be noted that the merged and "non-dispersed," (due to Meyer's loop) contralateral images projected to the striate cortex no longer contain the information necessary to extract a stereopsis error signal.

The lower left portion of the figure shows all of the individual maps of the LGN and PGN as planar for convenience. It also shows the possible stereopsis errors as the shift between the location of the dotted plane and the equivalent colorless plane when it is

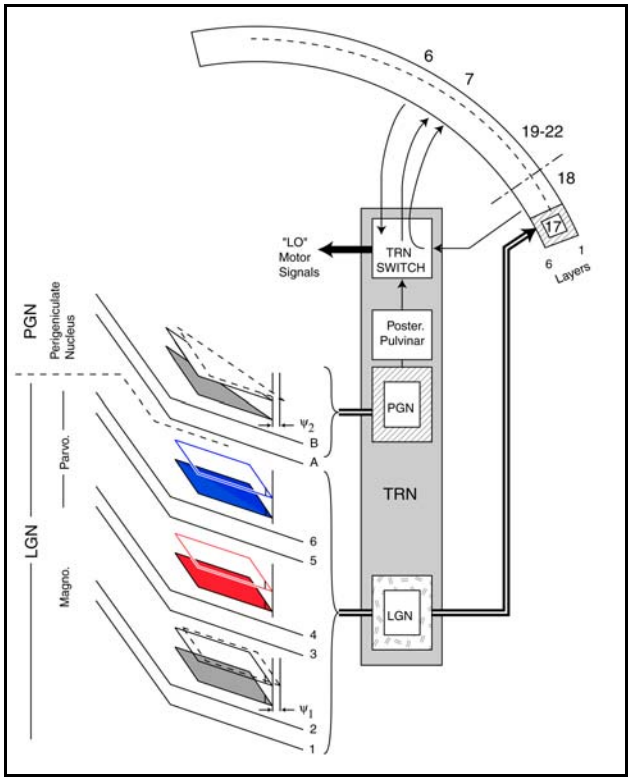

Figure 15.6.3-1 Functional organization of the TRN and associated structures.

[96]The term occipital and parietal lobes will be used here generally. Some readers may wish to inject the temporal lobe into the discussion. Others use the notation P-O-T to describe the morphological area being discussed.

properly aligned to the colored plane.

While well studied, the role of the LGN in higher cognitive processes is quite limited. It will not be discussed further in this section.

15.6.3.2 First order analysis of tasks assigned to the PGN/pulvinar couple

First order analysis of tasks assigned to the PGN/pulvinar couple

The two PGN's of the PGN/pulvinar couples are provided two individual contralateral images of one-half of the foveola. These images have been converged to the best ability of the LGN-POS servoloop. The PGN/pulvinar couple has the tasks of:

1. Further converging the two contralateral image pairs,
2. Merging the converged image pairs into two composite images
3. Merging the two composite images into a single representation of the foveola
4. Extracting the features of the single image of the foveola in cooperation with the POS. (operating in tremor mode)
5. Converting the characteristics of the features into a machine language interp
6. Probably assembling the individual interps into a global interp.
7. Placing the global interp into a saliency map, or
8. Forwarding the global interps to the saliency map maintained in the P-O-T

All of the above tasks seem compatible with the neural architecture and topology of these morphological elements. The task is to compare candidate mechanisms and processes with the known features of the PGN/pulvinar couple. This comparison should lead to a better understanding of the human system. The topography and neural architecture of the PGN are well suited to tasks 1 through 4. Tasks 5 through 6 appear well suited to the functions of a two-stage lookup table. Further analysis is required before choosing between tasks 7 and 8.

The complex neural circuitry of the PGN could be configured in a variety of ways to accomplish tasks 1 through 4. While the time dispersal of the input signals is not available as in the case of the LGN, an alternate mechanism is available. The motion known as tremor can provide a coherent scanning mechanism that can be used to present time dependent signals representing edges in the applied imagery. These signals can easily be used to extract stereopsis error signals. Once the images provided to each PGN are converged, a summation process, on a pixel-by-pixel basis, leads to a composite image. With two composite images available, two possibilities appear. The two composite images can be merged into a single image, traceable to the foveola, and the features can then be extracted. Alternately, the features can be extracted from each composite image and a merging of features can be performed in abstract space.

15.6.3.3 The PGN/pulvinar as the precision feature extraction engine of human vision

This section will combine parts of the top level schematics and top-level functional diagrams of PART I of this chapter with the frameworks of [**Figures 15.4.1-1** and **15.6.3.2-1**] and the information in the literature concerning the PGN and pulvinar. The goal is to obtain a better understanding of the role played by the PGN/pulvinar couple. Following the discussion in this section, **Section 15.6.4** will assemble a new set of top-level schematics and functional diagrams to provide a more comprehensive view of the human visual system.

15.6.3.3.1 Proposed signal architecture near the PGN/pulvinar couple

Figure 15.6.3-2 provides additional background on the overall visuotopic projection to the PGN/pulvinar couple. Overall architectural considerations suggest there are at least two options related to the signal chain. In Option 1, the features projected onto each side of the foveola are extracted by the PGN and the initial abstract signals representing the features are combined in a merging operation. The initial interps are then extracted from the merged data in one of two pulvinar regions before being assembled into global interps for transmission to area 7 of the neo-cortex. In Option 2, the images projected onto each side of the foveola are merged into a single visuotopic map before the extraction process begins. The extracted features are then converted into initial interps and global interps within a single region of the pulvinar. The labels above the figure describe the nature of the computational anatomy found below them. Also described are the states of signal dispersion found below the labels.

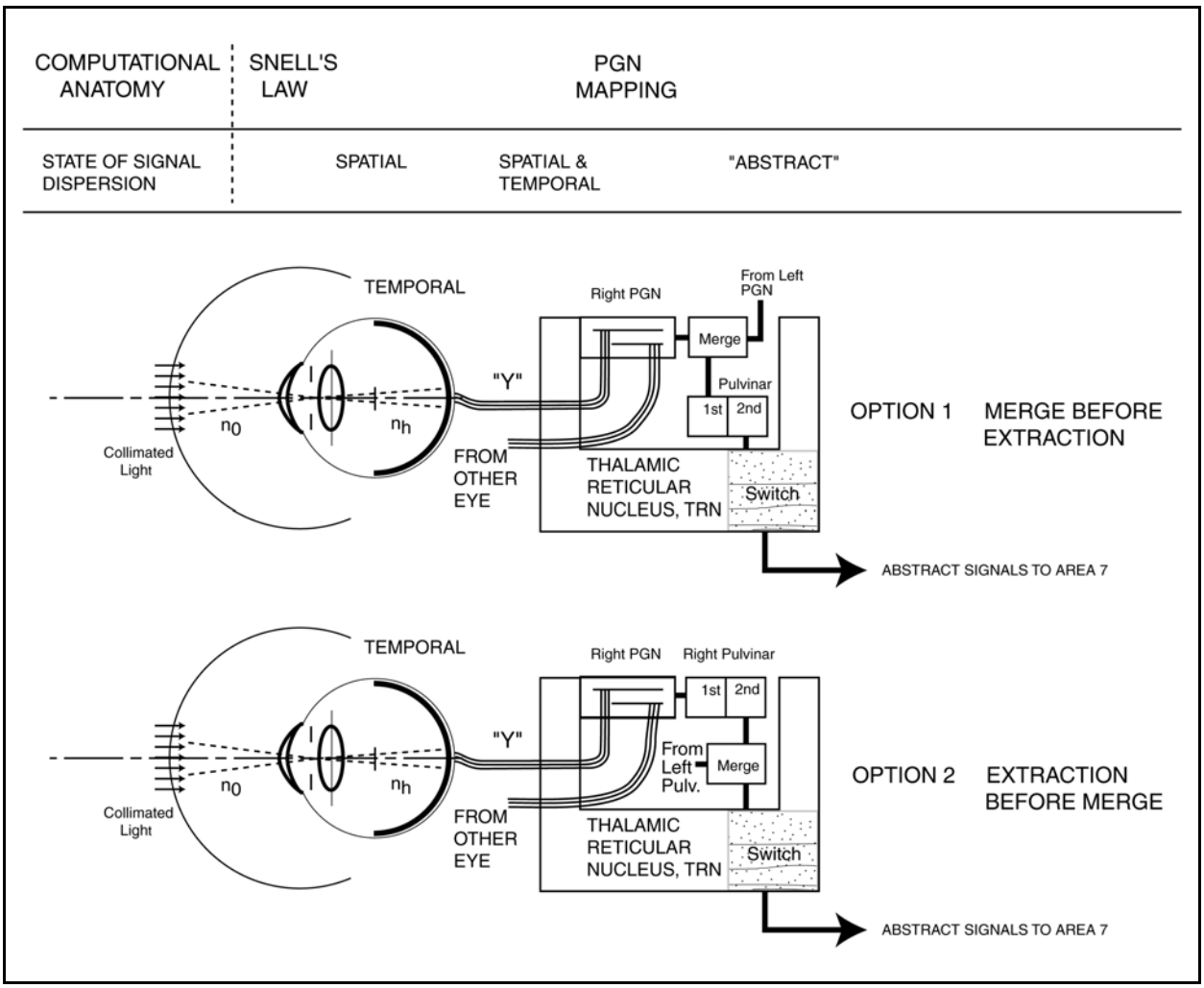

Figure 15.6.3-2 DUPL Steps in the creation of a visuotopic representation at the PGN/pulvinar couple. Two options are shown. In option 1, the signals from the two PGN's are merged into one map before the features are extracted. In option 2, the features are extracted from the map in each PGN before the signals are merged into a single stream of interps. The key location of the TRN is shown. Signals pass through its supervisory portion to reach the PGN. They are processed in the PGN portion and then pass through its switching portion to reach the neo-cortex. Snell's Law only impacts the scale of the image on the retina. The signals from the retina are labeled "Y" to indicate they are signals from the photoreceptors that have bypassed the signal processing of stage 2. See text.

This figure is assembled from those developed earlier in **Sections 2.4.1, 2.6.1, 2.8.1** & **15.2.5**. Because of the difference in index of refraction between air and the viscous humor of the eye, the image on the foveola of the retina is scaled by Snell's Law. The signals from the retina are labeled "Y" to show they come directly from the photoreceptor cells and bypass any stage 2 signal processing. Thus, they may be either S-, M- or L-channel signals but they are treated as if they are achromatic in the PGN. Under a stable state of adaptation, and with a light source of sufficiently high color temperature, the monophasic analog signals from all of these channels are of the same amplitude. The signals imaged on the foveola from the left half of object space are delivered to the right PGN. Those from each eye are delivered to individual layers of the visuotopic map (equivalent to the retinotopic map, except for a matter of scale, under the paraxial assumption). Under each option, the signals are processed within a merging circuit and two stages of pulvinar processing as suggested by the overall architecture. No element has been isolated morphologically or electrophysiologically that is known to perform the merging function. Although elements of the pulvinar might perform the 1st and 2nd level interp formation, there has been no verification of such a mechanism. Identifying the merging and extraction circuits will be very difficult in the short term because of the abstract nature of the signals describing the features and interps, and the fact they may involve multiple neural circuits operating in parallel. Decrypting the machine language code used by the brain may be necessary before

major progress can be made in this area.

The visual system is called upon to identify and extract features from images centered on the point of fixation of the retina. However, the relationship between the point of fixation and the spatial division of the foveola with regard to signals transmitted to the two PGN's is not well established. If the point of fixation is aligned with the division between the two hemifields of the foveola, it is likely that the visuotopic maps from the two PGN's will be merged before feature extraction occurs. If true, the primary role of the PGN's will be similar to that of the LGN's, extract a precision stereopsis signal and create a composite image representing one half of the image applied to the foveola. Under this scenario, the initial feature extraction function will occur either in another area of the TRN or in the pulvinar. An analysis of the neuroanatomy and topology of the PGN's may help answer this question. This subject will be discussed in detail in **Section 15.6.3.4**.

In processing the information from the foveola, the received signals are coded in time depending on the scanning pattern introduced by tremor, as discussed in **Sections 7.3.8** & **15.6.6.2.1**. This subject will also be discussed in detail in **Section 15.6.3.4**.

Notice that the signals extracted from the foveola by the PGN do not go to the "primary visual cortex," but go directly to area 7 of the *neo*-cortex.

15.6.3.4 The perigeniculate nucleus as the correlator of analytical mode vision

This section will discuss the neuroanatomy and topology of the PGN leading to the extraction of features from the visuotopic signals presented to the PGN's. It will continue to use option 1 of **Section 15.6.3.3.1** as a baseline.

The most obvious feature of the TRN is its great variation in properties, both superficial and volumetrically. The perigeniculate nuclei form quite distinct areas (compartments) of this element. The PGN's are hybrids in the sense that they are not clearly organized as a sheet like in the *neo*-cortex nor can they be described as largely volumetric structures.

The above papers provide a wealth of morphological, neuroanatomical and electrophysiological data but very little on the architecture or topology of the PGN's. While at least one paper suggests the PGN was originally a part of the LGN, and retreated from it, the image from Benson, et. al. showing the optic nerve between the two elements suggests otherwise. The more widely held view that the PGN is a compartment of the TRN and that the TRN is derived from the ventral thalamus, will be supported here.

Looking at only a putative multi-dimensional correlator within the thalamic reticular nucleus, it has been found that there are pathways between the portion of the optic nerve dedicated to the foveola and this nucleus[97]. Such a pathway would not need to be robust to accommodate a nominal 23,000 neural paths from the foveola. Furthermore, the area of the overall nucleus required to provide such a correlation function (probably 10 million neurons or less) could be measured in square millimeters or less. The remainder of the nucleus could be left to other integration functions and the control point. It is also noted that most of the neural paths to the thalamic reticular nucleus come from the dorsal thalamus. Sherman & Guillery briefly discuss the potential for correlation within such a structure on page 102.

15.6.3.4.1 The neuroanatomy and topology of the perigeniculate nucleus

As the TRN approaches the LGN, a section of it changes in its spatial organization. This unique region has been named the perigeniculate nucleus, PGN, because of its functional similarity to the LGN, its physical similarity to the TRN and its unusual spatial mapping. The exact forms of the TRN, and its extension, the PGN, are difficult to specify using two-dimensional slices and two-dimensional figures. Benson, et. al. provide the best description found[98]. Their figure 2 frames 6, 7 & 8 show the TRN passing to either side of the PGN depending on location but do not show continuity between them. Their figure 7 frame B suggests continuity between the TRN and PGN. Their figure 9 frame A is the most descriptive. It shows the optic nerve sandwiched between the LGN and the PGN. Whether the PGN exhibits a reticular character is not known.

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[97]Cucchiaro, J. Uhlrich, D. & Sherman, S. (1993) Ultrastructure of synapses from the pretectum in the A-lamina of the cat's lateral geniculate nucleus. *J. Comp. Neurol*. vol. 334, pp 618-630

[98]Benson, D. et. al. (1991) Op. Cit.

Very little information has been published concerning the neuroanatomy or topology of the PGN. Sherman & Guillery say the cells of the PGN have receptive fields that are in register with those of the LGN. However, the comment only refers to a caricature. The PGN in Benson does not share the same extent as the LGN and any similarity in alignment appears superficial since it only covers a part of the LGN. Empirical data is sorely lacking on the visuotopic extent of the map within the PGN and the related magnification factor as a function of location and direction (see **Section 15.6.5.2.4**). This work proposes the map only represents the foveola but the topology is of finer visuotopic resolution than in the LGN. It also proposes the PGN's contain a layer associated with the foveola of each eye. The thickness of the PGN is difficult to determine from Benson, et. al. It may approximate the two magnocellular layers of the LGN combined, or it may be thinner. No stratification of the PGN into two layers can be seen in their figures.

The location and similarity of the PGN compared with the LGN suggest similar roles. Specifically, it appears the PGN could provide a precision stereopsis signal using circuitry very similar to that providing the coarse signal in the LGN. The location of the PGN next to part of the pulvinar suggests that it might also cooperate in the extraction of features from the imagery projected onto the foveola.

15.6.3.4.2 Proposed functional tasks of the perigeniculates

The tasks required of the PGN's appear similar to those of the LGN's, and possibly the striate cortex combined.

1. As discussed in **Section 15.6.5.1**, there are two primary requirements placed on the LGN's. The first requirement on the LGN is to provide alarm mode, and vergence error, signals to the control point portion of the thalamic reticular nucleus. The second requirement is to provide merged luminance, chrominance (and other channel data if present) to area 17 of the occipital lobe.

2. The purpose of the PGN portion is to discover and extract the relationships between adjacent features in the imagery obtained from the foveola. The goal is to locate edges and endpoints. These are the critical elements in creating the initial interp needed to begin the interpretation process in biological vision.

3. The retinotopic maps of the LGN, based on luminance and chrominance signals, exhibit less resolution than the equivalent maps of the PGN that are based on the responses of individual photoreceptors.

4. Both the LGN and PGN manipulate differential data with respect to time. Because of the conversion of spatial information to time related data, the LGN and PGN can be considered to be processing spatial change data also. These engines do not respond to non-changing scenes.

5. The time difference between the appearance of a signal, due to an individual scene element, in the retinal map from one eye compared with the other is a precise indication of the vergence error related to that element. By averaging this error over the entire area of the field of view, an average vergence error is obtained. This error is fed to the POS via the TRN.

6. The vergence error of a scene element, relative to the average vergence error, is the parameter used to describe the range to the element in a three-dimensional interpretation of the scene.

These requirements call for a multidimensional correlator but do not necessarily call for feature extraction. On the other hand, the striate cortex appears responsible for feature extraction from the merged visuotopic map of the peripheral retina. This function can be achieved with the same multidimensional correlator if additional sensing lines are added. It is proposed that the PGN will be found to contain these sensing lines. It will also be proposed that the parallel outputs from these lines are transferred to the pulvinar for further processing.

15.6.3.5 Proposed generation of signals by the correlator

It is widely reported that large numbers of neurons are activated within the thalamic elements by relatively simple images projected onto the retina. However, little discussion could be found in the literature describing the signaling operation of the PGN or the pulvinar. What is completely missing from the literature is any discussion of the important role that tremor plays in creating a set of synchronous signals at the output of the photoreceptor cells. These signals are optimally processed in the precision optical system, that includes the PGN/pulvinar couples, for two purposes. The first is to extract the features from the signals from the retina and produce the interps and percepts provided to the saliency map of the brain. It should be noted that the synchronous nature of the signals from the periphery of the retina are not recognized by the LGN's because of their coarser processing resolution.

The model of this work provides considerable information, consistent with the meager literature related to signaling, on the operation of the PGN (and also the LGN) as signal extraction correlators.

15.6.3.5.1 Generation of a precision stereopsis signal

Figure 15.6.3-3 illustrates the ease of extraction of a precision stereopsis signal on the basis of the tremor of the visual system and individual pairs of photoreceptors in the same relative position in each eye. The top frame represents a vertical bar pattern near the point of fixation in object space. The spatial positions of the edges are shown in terms of time. This time is indirectly proportional to the nominal velocity of the tremor. The bottom frame shows the programmed motion of the two eyes (assuming the box-scanning format of **Section 7.3.8**) according to the assumed linear tremor displacement profile. The middle two frames show the nominal response of each eye in the presence of a stereopsis error based on the photoreceptors as edge detectors (see Section **15.1.4.6**). The upper of the two frames shows the positive-going response of the photoreceptor cell. It is shown occurring at an earlier than nominal time. The lower of the two frames is similar, but the response occurs after the nominal time. In both cases, the width of a single photoreceptor cell is shown by the total time of the rising wavefront. At the point where each signal amplitude reaches a threshold (actually an equivalent threshold reflecting the threshold at the ganglion cell of the signal projection stage–stage 3), an action potential will be initiated within the retina. These will be transmitted over nominally equal length paths to the same PGN. Assuming the two signals terminate in separate visuotopic images, a "boxcar generator" circuit can easily generate a square wave signal with a width proportional to the difference in arrival time of the two signals. Two such generators, operating in opposition, provide a pair of signals completely defining the relative error in stereopsis between the two cells. Notice that the time differential between these two signals can be much better than the time equivalent to the diameter of a photoreceptor cell. Furthermore, this same process can be employed using many pairs of cells. If the average pulse width output by the ensemble of boxcar generators is computed, a very high signal-to-noise signal can be obtained. These precision signals can be used to null any residual vergence error via the precision optical system, POS. After nulling this error, the location of the vertical edge in space is known precisely in time. This time provides a precise estimate of the vertical edge relative to the point of fixation in object space.

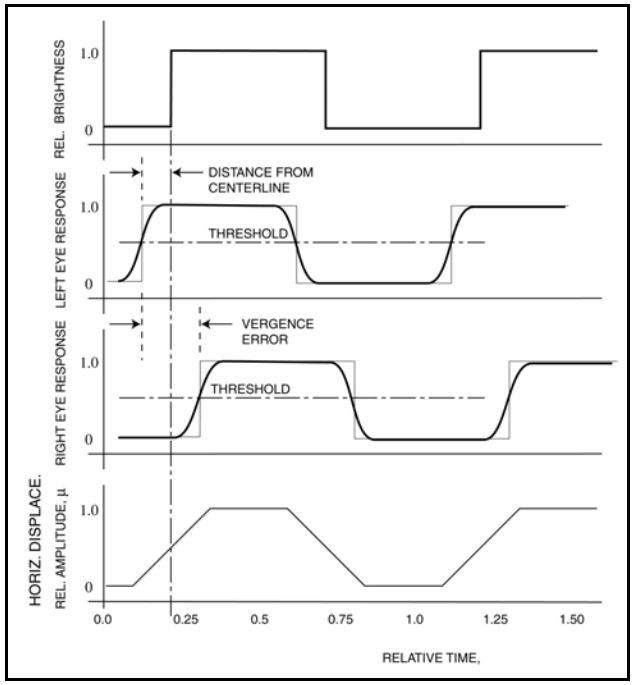

Figure 15.6.3-3 Generation of precision vergence errors and other signals. See text.

The boxcar generators need not be individual circuits, their function is easily incorporated into a larger correlator of the type developed conceptually in **Sections 15.5.2** and described topologically in **Section 15.6.3.4**.

While the leading edge can be used to generate an action potential, the trailing edge will not for several reasons. First, a decreasing amplitude signal will pass through the equivalent threshold level. By going below the threshold, it will normally stop a burst of action potentials. For the photoreceptors of the foveola, each sweep of the image across the photoreceptor occurs in a very short time (under POS control). It can be assumed that only one action potential will be generated during the duration of one sweep. As a result, there will be no burst of action potentials when examining the finest details of a scene. It is likely that the falling edge of the signal will occur during the refractory period of the ganglion cell.

The above scenario is in consonance with the well-known fact that the visual system can only differentiate between dark and light at the limit of its acuity. The presence or absence of a single temporally synchronous action potential provides this differentiation.

15.6.3.5.2 Proposed topology of the PGN

There are a variety of topologies that might be found in the PGN. It is too early to speculate on which topology is used in practice. It is necessary to first discover the division of labor between the pulvinar and the PGN.

It appears the topology of each PGN must support the merging of two images representing either the left or right half of the foveola. It also appears the topology must accommodate two or more time sequential frames of each image (or of the merged image). These images would be related to the different phases oculomotion related to the tremor of the eyes. It is expected that the visuotopic extent of each image will be a hemifield of about one degree diameter. The granularity of the neural network should support one pixel for each photoreceptor in the hemifield, about 12,000 pixels. No information is available concerning any computational anatomy associated with the optic nerve leading to each PGN.

15.6.3.5.3 Initial extraction of features

The above discussion can be extended from detecting a vertical edge to detecting the presence of multiple vertical edges of finite separation and finite length. It can be further extended to detect the presence of horizontal edges also, but this discussion will focus on a one-dimensional scenario for simplicity. If both horizontal and vertical edges are examined, the quality of the corners becomes important as discussed in **Section 15.1.4.6.**

The detection of vertical edges is accomplished by employing columns of photoreceptors in the two retinas. The signals from the columns are both merged and correlated in a multi-dimensional correlator (instead of using individual boxcar circuits) of the type discussed in **Section 15.5.2**. Individual neurons, acting as amplifiers, may be employed at each cross point of the correlator. Using an amplifier at these locations allows the use of many sensing lines. Under this condition, many neurons may be excited due to the many input lines that are excited. However, the output of the correlator may only consist of a few signals meeting the criteria imposed by the topology of the sense lines. The signals representing a single correlation will appear on multiple signal paths (neural axons). The signals may or may not be phasic in character. The fact that many of them are in analog mode makes it very difficult to isolate and measure them, using current techniques.

As with forming the precision stereopsis signal, the output of the correlator, describing scene features, consists of multiple parallel signals that are in synchronism with the tremor signal. Each set of signals exists for the nominal period of one action potential (the typical case for a non-return-to-zero code). Each set of signals defines the presence of one or more lines in the image projected on the foveola, and the spacing (not necessarily equal) between the lines if appropriate.

The often noted multiple distinct states of "output" for the ganglion cells of the TRN and PGN are quite compatible with the Boolean algebra performed by these nuclei. Only with sufficient correlation between the input signals and the test configuration will a super-threshold condition result in a phasic response. In general, each individual action potential produced carries a part (one bit) of the output message. Sequences of action potentials at a spacing of about eight milliseconds merely indicate multiple outputs as the result of individual correlation cycles. Under these conditions, the complete output message in "machine language," and designated a vector, occurs on a series of ganglion axons simultaneously. The message is transmitted as a parallel word over multiple axons grouped into one (portion of a) commissure. See McCormick, et. al. for details concerning the waveforms associated with a single ganglion cell[99]. To record the complete "machine language" vector would require finding and simultaneously interrogating the multiple neurons associated with the above vector. This is the normal procedure in troubleshooting modern communications equipment. Of course, in that case, the particular signal channels that are relevant are known in advance from the circuit diagram for the equipment.

Using the dimensions of the correlator discussed above, the PGN can extract the features of an area roughly one degree in diameter in one cycle of the tremor signal. If the signal-to-noise ratio is less than desired, the system can take several actions. It can repeat the correlation process or concentrate more intently on a specific portion of the field. Alternately, it can move the eyes, head or body to obtain a more favorable perspective on the object in object space. These are the secondary tasks associated with the analytical mode (and the key initial steps in reading).

Different written languages have adopted different symbology to optimize the reading process further. They employ at least two obvious techniques. They limit the region of the foveola used to describe one syllable or pictogram. They also stylize the lines using different stroke widths (profiles) and introducing serifs, etc.

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[99]McCormick, D. Huguenard, J. Bal, T. & Pape, H. (1997) Electrophysiological and pharmacological properties of thalamic GABAergic neurons. *In* Steriade, M. Jones, E. & McCormick, D. Thalamus, vol. 2, pp 163-169

15.6.3.5.4 The effective size of the correlator of the PGN

McKee has provided substantial data deliminating the size of the correlator in terms of distance in object space[100]. Her data strongly supports a correlator operating over a diameter of not less than 0.75 degrees based on stereoacuity measurements.

15.6.3.6 Roles of the pulvinar in vision

Quoting Cooper, et. al[101]. in 1974, "The pulvinar is the most posterior and the largest of the thalamic nuclei in humans . . . It becomes well defined in primates but only in man does the pulvinar attain massive size . . . So little is known about the function of the pulvinar that Walker has referred to it as the terra incognita of the thalamus." This largely remains the situation today. It is interesting to compare this statement with that of Sherman & Guillery (2001) that the thalamus itself is the terra incognita of the cortex. Robinson & Cowie have provided a broad discussion of the role of the pulvinar in vision[102]. However, they do not discuss signaling directly. According to them, "Our general theme will be that the pulvinar is organized to contribute signals which indicate the salience of visual images and events." Further, "however, the salience of visual events is determined, it is our hypothesis that the pulvinar plays a critical role."

While Robinson & Cowie claim the presence of several visuotopic maps within the pulvinar, they do not differentiate clearly between the receptive field versus visuotopic aspects of these maps. When discussing the dorsal and medial pulvinar, they made several observations. They speak of visually excitable tissue and "large visual receptive fields which do not follow a strict topography; if this area has a retinotopic order, it is very crude."

Robinson & Cowie have made an interesting observation. "These data suggest that the saliency function of the pulvinar need not work on visual information which is presently being processed within the visual pathway but can also work on visual data retrieved from memory." The nature of this memory will be developed further below. They also note a relationship between the pulvinar and eye movements but do not define the relationship. They do provide a caricature of eye movements in response to different alarm type stimuli in object space. It shows some similarity to the previous figure describing formation of the stereopsis signals in the LGN and PGN. They provide a short discussion of the high activity level in the pulvinar within milliseconds of an eye movement. Their discussion then turns to the tectal-pulvinar pathway. However, it is focused on the lower mammals and reflects some of the same paradoxes as Murphy has addressed regarding the PGN in the cat. The performance of the human PGN/pulvinar couple and the signals carried over the pulvinar pathways cannot be ascertained from tests on the lower mammals (or even the lower primates).

Robinson & Cowie close with several qualifications to their original preposition concerning the role of the pulvinar role in generating saliency. "First of all, the pulvinar does not act alone in this function . . . Second, this is probably not the only function of the pulvinar . . . Finally, we have spoken of the pulvinar as if it were monolithic. Clearly, . . . show that the pulvinar has many different levels of organization." These corollaries are in excellent agreement with the discussion in the remainder of this section. Their concluding remarks concerning unresolved issues are also consistent with this work. They call for more work connecting the pulvinar to movement of the eyes and limbs. This work describes these relationships in detail in terms of the precision optical system, POS (see **Section 7.3**). They also call for more study to decide if a parallel can be drawn between the operation of the striate cortex and the pulvinar. This work defines just such a parallel between the PGN/pulvinar couple and the striate/$_{V>2}$ couple (discussed in this major section and **Section 15.6.5.2**). In conjunction with **Section 2.8.1**, this work explains why serious damage or removal of the striate cortex does not result in obvious changes in the visual capability of many animals. Closer observation would show their loss of peripheral vision (and the awareness channel) but not the foveola vision (and the analytical channel).

Several authors have noted the bulk characteristics of the pulvinar and the small size of the neurons contained within it. This section will attempt to sift through the available information and extract the characteristics and features of this structure relevant to vision. Steriade, et. al. have noted several operational features associated with the pulvinar. These include its role in vision, visuomotor functions and attention. It also includes the fact that the pulvinar reacts **after** major oculomotor movements. Finally, they note the more than proportional growth in the size of the pulvinar with position in the phylogenic ladder of chordates and the very large size of the intralaminar nucleus in humans. They also note the significant connections between the pulvinar and the cerebellum. Multiple topological maps are

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[100]McKee, S. (1983) The spatial requirements for fine stereoacuity *Vision Res* vol. 23, no. 2, pp 191-198

[101]Cooper, I. S. et. al. (1974) Clinical physiology of motor contributions of the pulvinar in man. *In* The Pulvinar-LP complex. Springfield, IL: Charles C. Thomas. pg 200-201

[102]Robinson, D. & Cowie, R. (1997) Chapter two "The primate pulvinar: structural, functional, and behavioral components of visual salience." *In* Steriade, M. Jones, E. & McCormick, D. Op. Cit.

reported in the pulvinar. However, many of them appear to be maps of receptive fields rather than true visuotopic maps.

15.6.3.6.1 The neuroanatomy, topology and commissure of the pulvinar

As noted earlier, the pulvinar is a massive volumetric structure. It also appears to be deeply involved in processing signals involving parallel data words. These features make it extremely difficult to determine the topology of the pulvinar using single probe, and even dual probe, techniques. The challenge is to determine if the neuroanatomy and topology of the pulvinar is compatible with the architecture applicable to the PGN/pulvinar couple. In analyzing these parameters of the pulvinar, an answer to the choice between option 1 and option 2 introduced in **Section 15.6.3.3.1** may appear.

15.6.3.6.2 Role of the pulvinar in controlling attention

Robinson & Petersen have briefly discussed data showing the pulvinar plays a role in controlling, or determining the attention level in humans and monkeys[103]. The data is sparse but relevant. Their discussion of the operation in the presence of a cluttered object space can be interpreted in a variety of ways, as will become clear later. The activity level of a multi-dimensional correlator or a lookup table is directly related to the complexity of the image being processed. In the face of the other proposed tasks performed by the pulvinar, it is difficult to show the observed level of activity is related uniquely to attention. This work would suggest that it is the TRN that controls attention. Robinson & Petersen did not introduce the TRN into their discussion or address its possible role in attention. They do note the dorsomedial pulvinar is interconnected with area 7, which has traditionally been associated with spatial attention. However, any role for the pulvinar in attention remains primarily inferential.

15.6.3.6.3 Role of the posterior pulvinar in feature extraction

Mitrofanis & Guillery (‘93) address the three-dimensional nature of the elements within the thalamus and how they might relate to a two-dimensional visuotopic image from a global perspective. They also address the role of the thalamus in processing the signals from other modalities. They do make the following overly broad comment. “There is, therefore, an important and intriguing organizational change that occurs between the cortex and the diencephalon.”

Under option 1 in this work, the pulvinar is not asked to map visuotopic space but to provide a large lookup table. With this table, the pulvinar is able to correlate the basic interps obtained from the perigeniculate region of the TRN into a more comprehensive, and totally abstract, interp. This interp can be placed in the saliency map and passed to the parietal lobe of the *neo*-cortex. The number of dimensions of the pulvinar has no role to play in this correlation process. The number of dimensions involved in the signals from the PGN may far exceed three. The detailed function of the posterior pulvinar will be discussed in greater detail below.

Many investigators have noted that many neurons are excited within the posterior portion of the pulvinar when almost any stimulus is applied to (the center of) the retina. This is exactly what is expected when the individual neurons of a correlator have large receptive fields. These responses are then summed using Boolean algebra to determine the precise spatial nature of the actual stimulus. Only a very few output neurons respond because of this summation.

Ward et al. have recently provided psychophysics laboratory and MRI investigations into the ability of the pulvinar to extract scene information related to the small field of view of the foveola and the PGN/pulvinar couple[104]. They claim, “These results are the first evidence for spatiotopic maps at the rostral boundary of the human pulvinar, homologous in location and organization to the inferior and lateral maps of the monkey.” They also comment on the transfer of the extracted information to the parietal lobe. No mention of the occipital lobe occurs in this discussion.

Unfortunately, no effort was made to constrain the saccades of the eyes to insure limiting the image of the stimulus to the foveola. While the text discusses the binding problem briefly, the discussion is not substantive in that area.

15.6.4 THE EMERGING GROSS ARCHITECTURE of human vision, ca. 2002

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[103]Robinson, D. & Petersen, S. (1992) Op. Cit.

[104]Ward, R. Danziger, S. Owen, V. & Fafal, R. (2002) Deficits in spatial coding and feature binding following damage to spatiotopic maps in the human pulvinar Nature neurosci vol 5(2), pp 99-100

The historical architecture of the visual system has been encountering more and more problems during attempts to verify its applicability. The investigations into "blind sight" and the effect of a total commissurotomy of Trevarthen & Sperry[105] show operational capabilities that should not have been possible based on the historically assumed architecture. Furthermore, the recent work of the Conley and the Guillery schools have surfaced vast amounts of data that have no place in the historical architecture. They revolve around a portion of the thalamus, the thalamic reticular nucleus, that was virtually unreported in the vision literature before the mid 1980's. Finally the brief statement of Zeki can now be expanded based on the comments of the Guillery school. While Zeki said "there is no cortical region which is only recipient–all cortical areas have outputs as well as inputs." XXX went further and said the number of cortico-thalamic neurons, those returning to the thalamus, exceeds the number of thalamocortical neurons going to the primary visual cortex. This fact, combined with the striated nature of area 17 suggests a role considerably different from earlier assertions.

These situations call for a new architecture compatible with the available data. This architecture makes major changes in the roles played by the previously recognized elements of the CNS involved in vision.

By correlating the material analyzed during 2000 through 2002, and presented in **Sections 15.5** through **15.6.4**, with the material presented earlier in the chapter, new models of the operating aspects of vision in humans can be detailed. The differences will be highlighted in a series of new emerging diagrams derived from those presented earlier.

15.6.4.1 Emerging Top Level Schematic & Functional Diagram, ca. 2002

Figure 15.6.4-1 presents an expanded Emerging Top Level Schematic of human vision. The schematic is becoming unwieldy when presented in one figure. Many of the reciprocal paths now recognized between areas of the neo-cortex and the paleo-cortex have been omitted. Furthermore, the role of the thalamic reticular nucleus as the control center of the neural system has not been shown here. It will be shown in later figures in **Section 15.6.4**. This figure replaces the conceptual pretectum of the earlier figure with the more recently defined PGN/pulvinar couple and more clearly delineates the signals going to the PGN. This additional delineation gives further definition regard to the so-called "Y-signals" found primarily in the cat literature. The Y-signals is the name given to a group of signals from the foveola that are passed directly from the photoreceptor cells to the PGN without intermediate signal processing (other than propagation by the phasic circuits of stage 3). They provide a higher spatial resolution visuotopic image to the PGN. The signals represent all spectral bands of vision but they are treated as achromatic by the PGN. The emergent methodology involves two distinct visual processing subsystems. The first is a chromatic subsystem related to peripheral vision, concerned with the awareness mode of vision, and associated with the LGN and the striate cortex. The second is an achromatic but higher resolution subsystem related to foveola vision, concerned with the analytical mode of vision, and associated with the PGN and the pulvinar. The presence of these two largely independent subsystems explains many previous questions in the literature. The model agrees with the long recognized fact that the visual system near the line of fixation is "color-blind" with respect to fine detail. The perceived image of a small object near the point of fixation consists of the color specified by the peripheral subsystem but the detail specified by the analytical subsystem. The presence of these two systems also explains the ability of the system to operate well following complete destruction of the so-called, but inappropriately named primary visual cortex. A central field of something more than one degree diameter remains fully functional after destruction of the striate/$V_{>2}$ couple. On the other hand, the destruction of the PGN/pulvinar couple leaves the visual field unchanged but deprives the subject of the ability to recognize "grandmother." See also **Section 15.7.7**.

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[105]Trevarthen, C. & Sperry, R. (1973) Perceptual unity of the ambient visual field in human commissurotomy patients. *Brain*, vol. 96, pp 547-570

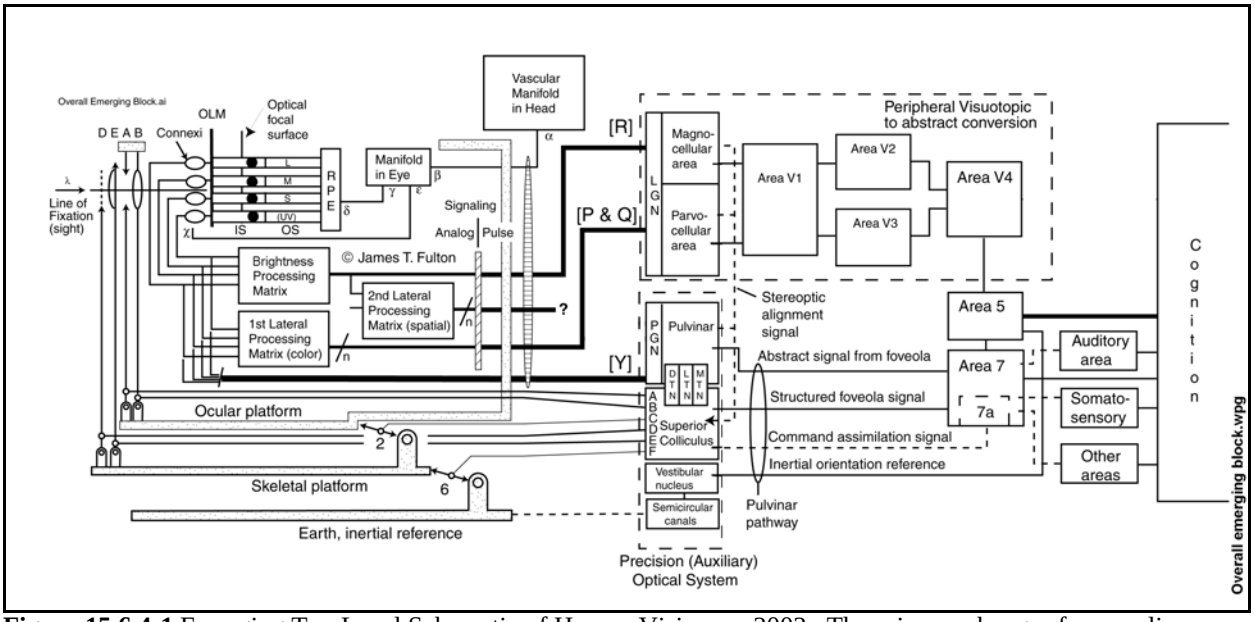

Figure 15.6.4-1 Emerging Top Level Schematic of Human Vision, ca 2002. The primary changes from earlier involve the further definition of the PGN/pulvinar couple replacing the largely conceptual pretectum. Other changes relate to the delivery of spectral signals from the photoreceptors directly to the PGN (over the Y-channel). This change allows explicit labeling of the P, Q, and R. channels in accordance with this work. The role of any 2nd lateral processing matrix in human vision remains questionable. Also questionable is the delivery of any chromatic information to the PGN.

It has been shown that these two subsystems employ different techniques regarding the generation of the stereopsis signals required to focus on nearby objects. The peripheral (awareness mode) subsystem relies upon time dispersal related to the position of individual photoreceptors in the retina. The foveola (analytical mode) subsystem is integrated into the closed loop precision optical system, POS, and relies on time differences related to the scanning of the eyes produced by the microsaccades of the eyes known as tremor. As a result, the analytical mode of vision operates in a synchronous manner while the awareness mode does not.

As in the previous versions of this figure, the role or even existence of the second lateral processing matrix (spatial) remains questionable in humans. It appears to play a larger role in some animals of prey among the true carnivores.

Figure 15.6.4-2 presents a top-level Functional Diagram that also emerges from the recent analyses of the literature. The new figure answers a broad range of questions left open in **Section 15.2.3.8**. The fundamental difference is the identification of the putative control point of the model as of 1998. This control point can now be identified as the predominant (but unnamed) compartment of the thalamic reticular nucleus. This compartment can be divided into two subcompartments. The one is the true control point supported by a memory element. The second is the switching matrix that has a configuration that can be changed by the control point. The critically important role of the thalamic reticular nucleus, TRN, leads to its becoming the center of the overall figure.

The figure shows one half the visual system with the signals from one eye entering from the left. The gray shaded area represents the large number of commissure traversing between the half of the system shown and the other half, shown in brief along the right edge of the figure. The figure remains focused on the visual system but has been drawn showing one half the aural modality along the top of the figure for comparison. As in the previous figure, the major delays associated with the stage 3 projection circuits is shown explicitly in the figure. As in the previous Top Level Schematic, the retinotopicity declines with distance from the retina in favor of abstract signaling in "machine language." Nearly all of the circuits shown under the heading "old brain" are parts of the diencephalon. The exceptions being the circuits associated with the command path. These are generally associated with the mesencephalon (the midbrain).

The unique difference in signaling in this figure relates to the great importance of the signals returning to the LGN from the occipital lobe. While the figure shows a signal path from the occipital lobe to the parietal lobe, its importance has not been quantified. Considerable data is available showing that the signal flow from area 18-19,

etc. back to the LGN exceeds data flowing to area 17 from the LGN. A similar condition has been found concerning the signal volume passing from the PGN to and from the pulvinar. These conditions suggest a fundamental change in the importance of the posterior occipital lobe. Whereas a direct path from the LGN to the occipital lobe and hence to the parietal lobe has long been assumed, this does not appear to be the case any longer. This point can be demonstrated by the time required for signals from the retina to reach area 7. The time delays associated with distance from the old brain to area 7 via the pulvinar pathway and those associated with the geniculo-calcerine pathway and then from area 17 to area 7 are quite different. Exploratory experiments have already established that some retinal signals arrive at area 7 before they arrive at area 17. These experiments need to be expanded to explore the signals from the foveola and from the periphery separately.

If the above experiments confirm the organization as shown in the figure, the pulvinar pathway becomes the primary path between the old brain and the parietal and anterior lobes of the *neo*-cortex. This pathway extends from the posterior of the thalamus to area 7 of the parietal lobe. Under this concept, the LGN and the posterior portion of the occipital lobe act as a couple in converting the retinotopic map of the peripheral retina into an abstract, “machine language” vector. This vector is suitable for introduction into the overall saliency map shared by the parietal and anterior lobes of the brain. These vectors are passed back to the TRN from the LGN/occipital couple.

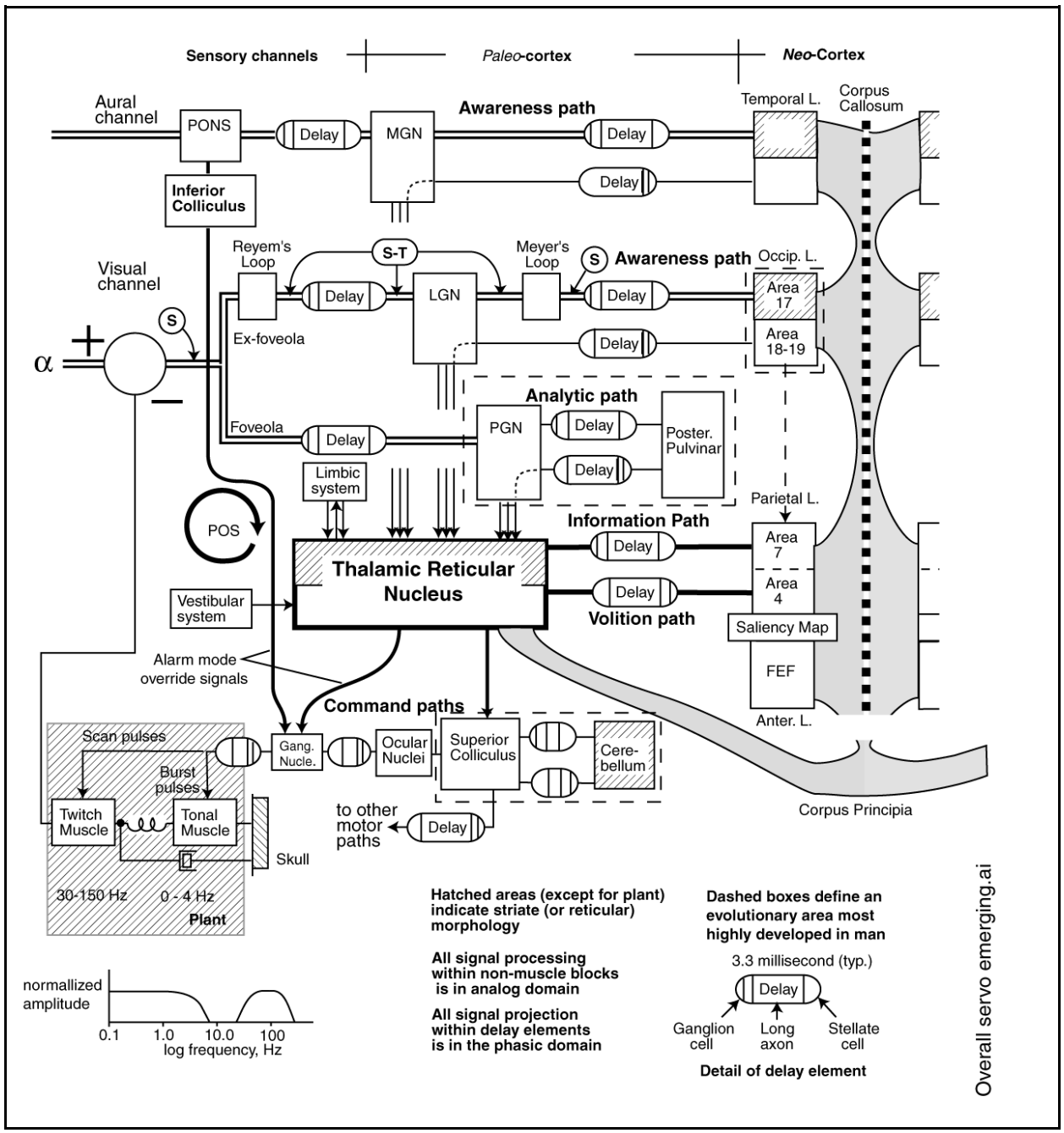

Figure 15.6.4-2 Emerging Top Level Functional Diagram of vision, ca. 2002. Also showing some related modalities. See text for extensive discussion. The corpus callosum and corpus principia are shown on the right connecting the two halves of the brain. As shown by Trevanthen & Sperry and others, cutting the corpus callosum along the dotted line does not seriously impact operation of the brain. Cutting the corpus principia (part of the internal capsule) has major implications.

couple to the TRN for forwarding to area 7 of the parietal lobe. As in the previous version, multiple types of signals pass from the LGN to the TRN (a.k.a., control point). The LGN initially extracts a signal indicating the current error in stereopsis. This signal is passed to the POS via the TRN. The LGN also extracts alarm signals, related to rapidly changing light intensities in object space. These signals are transferred to the TRN on a priority basis. Finally, the interps prepared by the LGN/occipital couple are passed to the TRN for further transmission to the higher cognitive

centers. Besides these three types of signals, it is likely that additional supervisory signals are sent to the TRN describing the state diagram being used by the LGN/occipital couple. Supervisory signals may also be sent from the TRN to each couple. These signals would instruct them to operate under a specific state diagram.

As in the earlier version, the encircled letters along the awareness path describe the state of the signals carried by that path. The signals from the retina are obviously related to their spatial position (S) in the retina. Because of differences in distance between the originating photoreceptor and the blind spot (shown as Reyem's Loop, and the finite signal velocity of the projection path, they also become dispersed in time (T). This time dispersal is of value in the LGN where it is a factor in the generation of the stereopsis and alarm signals. Following the LGN, Meyer's Loop is arranged to remove the dispersion in time so the spatial data can be processed without temporal perturbation. The same mechanism may be used for the signals from the foveola. However, the presence of such loops would be less obvious morphologically.

As developed in an earlier section, the TRN also plays a major role regarding the limbic system. While the limbic system may operate largely independently of the diencephalon in determining the physiological and emotional state of the individual, it appears the TRN plays a major role in the external expression of the emotional state of that individual. Thus, the limbic system is also shown interfacing with the TRN.

To avoid over complicating the diagram, a troika of signals is shown being passed from the MGN, the LGN and the PGN to the TRN. For the limbic system, the arrows are shown going both ways.

The figure shows most of the signals, including those related to the **awareness path** and the **analysis path**, going to the parietal and anterior lobes of the brain passing along the **information path**. This is a path not previously identified. The **volition path** remains as defined in the ca. 1998 figure. While no major signal path is shown between the anterior lobe, particularly the frontal eye fields, FEF, and the TRN, it is likely that supervisory signals are traversing such a path. However, most of the **instructions** prepared in the anterior lobe require conversion into complete **volition commands** by the parietal lobe (the premotor areas) before transmission to the TRN. Once transmitted as **volition commands**, and passed to the superior colliculus/cerebellum, the SC/cerebellum can convert the volition commands into complete commands suitable for exciting the motor neuron **command pathways**. In a sense the conversion of instructions into detailed commands reverses the process involved in reducing the retinotopic signals into abstract signals. The instructions are highly abstract. On the other hand, the neuron commands are directly relatable to the line of fixation of the eyes and the alignment of the skeletal frame of the organism.

The dotted box surrounding the PGN and posterior pulvinar represents the portion of the brain most highly developed in man, compared with the other animals. The development of this region is highest in the prosimian and simian species. In man, most of the pulvinar, by volume, appears dedicated to vision. This preeminence is much less in the lower mammals.

Several boxes in the figure, other than that of the plant in the lower corner, are hatched. These boxes represent morphological features that are either striated or reticulated. They also conform to elements that involve unique patterns of axons and neurites that can be associated with a correlation or switching function. This internal patterning of axons and neurites appears to be the reason for the observable surface texture of these elements.

The figure stresses the fact that the neo-cortex is less monolithic than described in many earlier works. There appears to be a division of labor between the different lobes defined by the major sulci.

The lower part of the figure remains the same as in the 1998 variant. The operation of the Precision Optical System, POS, servo-loop is suggested by the loop on the left of the figure. While gross signals from the MGN and LGN are used by the TRN for coarse pointing of the line of fixation, the precision operation of the system relies upon the signals derived from the foveola by the PGN. An interesting explanation for the existence of the ganglion nucleus along the command path to the oculomotor muscles has appeared in the ca. 2002 variant. It is suggested by the curved command path. To avoid potential catastrophes, alarm signals generated by the MGN and the LGN can be passed by the TRN directly to the oculomotor muscles (via the ganglion nucleus of the oculomotor nerve). This path avoids the time delay associated with the SC/cerebellum signal path.

15.6.4.2 Profile view of the visual topology of human and other primates, ca. '02

Figure 15.6.4-3 is an updated version of the similar figure in **Section 15.2.3**. It differs primarily;
1. in identifying the largely putative pretectum in man with the recently documented perigeniculate nucleus portion of the thalamic reticular nucleus,
2. in recognizing the significant flow of abstract data from the posterior occipital lobe to the LGN (probably separate from Meyer's Loop),
3. in eliminating the major signal path from the posterior occipital lobe to the parietal lobe, **and**
4. in recognizing the crucial role the TRN plays in vision.

It also shows all of the retinal neurons passing through the TRN having collaterals that terminate in the TRN. The perigeniculate nucleus, PGN is coupled with the pulvinar. The superior colliculus is shown coupled with the cerebellum. The elements of the POS are shown as those bordering on the circular symbol at lower left in the inset.

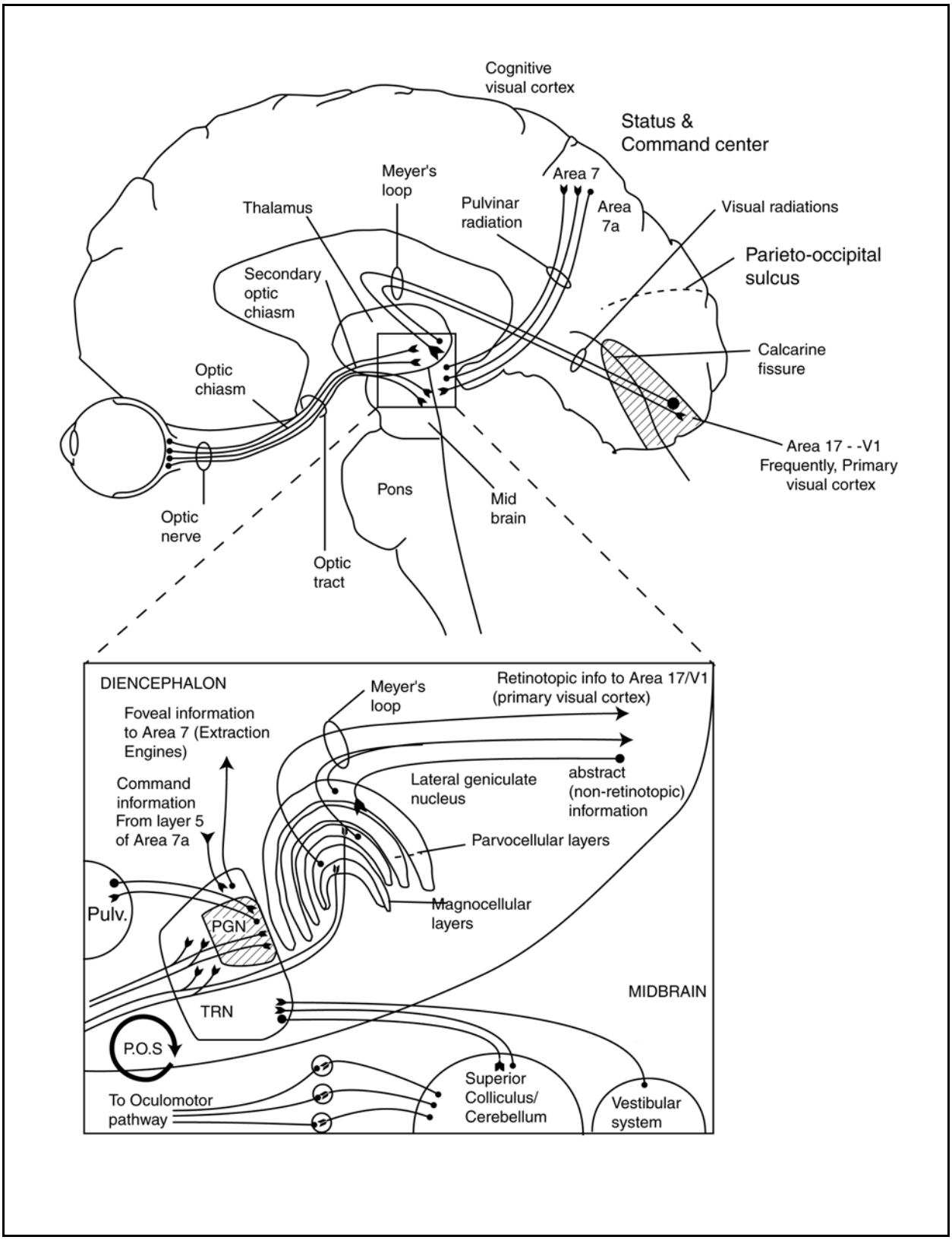

Figure 15.6.4-3 Emerging profile view of the visual system in humans, ca. 2002. The previous signal path from area 17 to area 7 has been removed and the flow of abstract data back to the LGN from the posterior lobe has been emphasized. The inset has been redrawn to emphasize the role of the thalamic reticular nucleus.

15.6.4.3 Plan view of the visual topology of human and other primates, ca. '02

Figure 15.6.4-4 is a major expansion of [**Figure 15.2.3-2**] showing a plan view of the human vision system (arbitrarily shown from the top, although frequently shown from the bottom in photographs). Because the figure has grown in complexity, the previous variant may be used for orientation purposes. The major changes are two. The detailing of the thalamic reticular nucleus surrounding the thalamus is the most important. The caricature dividing the major commissure into the corpus callosum and the corpus principia leads to a better understanding of the operation of the overall system. The anterior hemispheres of the brain are shown with dashed lines for reference. They are separated from the posterior hemispheres by the central sulcus, CE. The posterior hemispheres are shown without the temporal lobes. The wings of the posterior hemispheres represent the parietal lobes. They are separated from the occipital lobes by the occipital-parietal sulcus, OP. The occipital lobes are in turn separated by the calcerine sulcus, CS. All of the lobes of the neo-cortex and the old brain are connected by various groupings of commissure. These are usually defined with respect to their location. The corpus callosum describes the great many commissure interconnecting the lobes of the left and right hemispheres of the brain. It is shown by the outer dark shaded structure. The corpus principia is another major group of commissure placed within the internal capsule that is found between the two lobes of the thalamus. It is shown as the inner dark shaded structure.

The thalamic reticular nucleus, TRN, is shown in simplified form as enclosing all of the thalamus and its internal components. It is shown by the lightly shaded structure. The major components of the thalamus are the left and right geniculate nuclei, serving vision, and the medial geniculate nuclei, serving hearing. Also included within the thalamus are the two pulvinar structures. The left and right perigeniculate nuclei are intrinsic portions of the TRN but can be considered as enclosed by the TRN. The couple formed by the superior colliculus and the cerebellum is shown outside the TRN. This couple is primarily involved in motor functions that include the motions of the eyes and skeleton. This couple respond to both volition commands and alarm-based commands according to a previously formed instruction set or state diagram.

Afferent signals are shown in the figure by solid lines. Nominally efferent signal paths are shown by dashed lines. For the afferent signals from each eye, the outer pair of traces represents signals from the left and right halves of the visual field, sans the foveola. The center trace represents the signals from the foveola. It is likely that this trace should also be drawn as two separate traces representing signals from the left and right half of the foveola. This depiction would complicate the drawing slightly. In the case of the triad of signals between the geniculate nuclei and the occipital lobe, one outer trace represents several million afferent signal paths. The other outer trace represents several million efferent paths. The central trace represents the supervisory channel between the two elements (which may incorporate signal paths in both directions).

As defined earlier, the left and right perigeniculate nucleus/pulvinar couples can be considered surrounded by the TRN. However, the striate/$V_{>2}$ couples are entirely outside of the TRN. The most important point is the crucial strategic location of the TRN. Nearly all neural paths involved in vision cross the TRN. It has access to all of these neural paths. It is this universal access that allows it to perform its supervisory function over all visual activity (which it also performs for other modalities). Although entirely external to the TRN, most neural paths leading from the pre-motor areas of the cerebrum to the superior colliculus/cerebellum couple also pass through the TRN. The signals emanating from the couple include both the oculomotor signal paths and all other skeletal motor signal paths.

The figure provides a more dramatic illustration of the results reported by Trevarthen & Sperry. As discussed earlier, the corpus callosum is used primarily to coordinate and merge information that straddles the fields of view of individual sensory channels. Destroying this very large and complex signaling channel does not materially incapacitate the individual. The corpus principia plays the more important role of controlling and coordinating the response of the organism. It does this in part by ranking the commands sent to the superior colliculus. Destroying this major signaling path has a catastrophic impact on the viability of the individual.

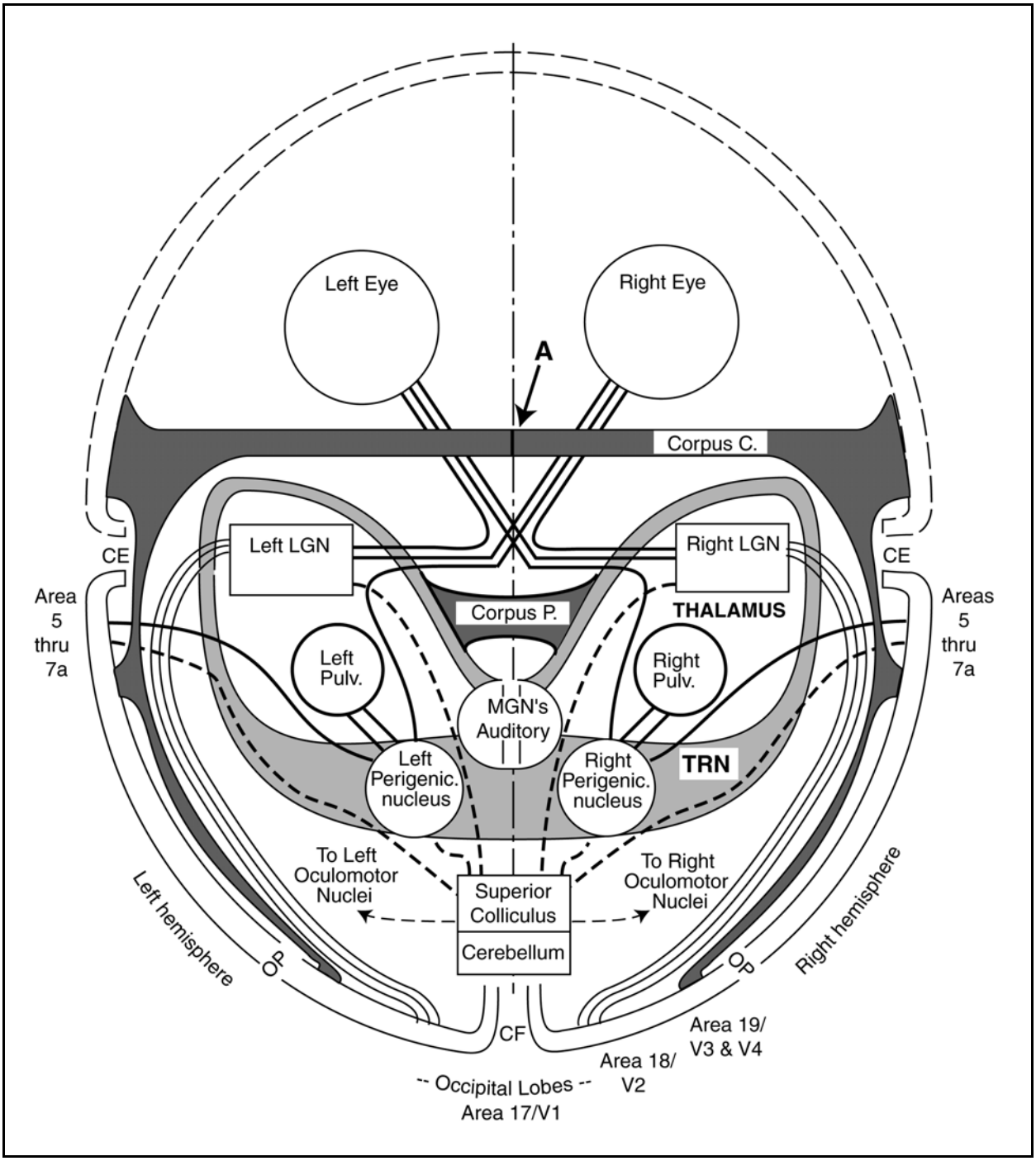

Figure 15.6.4-4 Emerging plan view of the human visual system, ca 2002. See text for extensive description. The ability of the TRN to access all of the neural paths going to and from the thalamus is crucial to its supervisory role.

15.6.4.4 Emerging top-level block diagram of the visual system, ca 2002

Figure 15.6.4-5 is emerging as the comprehensive block diagram of vision applicable to all biological vision. It illustrates a variety of relationships differently than do the Top Level Schematic and the Functional Diagram. Specific features in this diagram are absent from various species. The various blocks have been organized using a

series of step numbers for convenience in addressing certain relationships. As an example, the chordate retina does not contain polarization sensitive ultraviolet photoreceptors (as shown in steps 5, 6 & 7). The two UV channels shown are only represented by a single channel in these species. The utility of this channel has been drastically reduced in the larger mammals, such as humans, because of absorption of the UV by the lens group. However, the photoreceptors are still present as documented by aphakic observers. The spatial encoding matrix (step 10) is absent or residual in humans. However, it is very significant in other mammals, particularly the carnivorous animals of prey. It has been studied and documented extensively in the cat families.

The figure highlights the separate processing channel related to the foveola in the carnivores and arboreal animals (that includes humans). The development level of this channel is highly species dependent. It is most highly developed in humans, particularly in the capability of the pulvinar (step 16). Previously, the role of the diencephalon has not been clearly documented in the literature. Only the relay role of the LGN has been extensively studied (step 14). The additional critical roles of alarm signal and stereopsis signal generation have been largely overlooked. The roles of the PGN and the pulvinar have remained "terra incognita" to the present day.

The critical roles of the PGN/pulvinar couple and the striate/$V_{>2}$ couple have not been previously reported in a coherent and comprehensive manner. They are key elements in the perception of features related to scenes in object space. Similarly, the role of the superior colliculus/cerebellum couple in the operation of the efferent neural system has not been clearly described. Their role is complex and involves all afferent signal paths. While not discussed in detail, upon a failure within this couple, the TRN can switch the high level efferent signal paths from the P-O-T complex around the couple. Under these conditions, the organism displays awkward motions based on the unelaborated commands generated in the higher motor areas (step 18).

The omnipotent role of the thalamic reticular nucleus in vision has not been previously documented. This organ is the key control center in the entire neural system of any animal. It is known not only to be involved in emotion but to control the expression of emotions. Its role is actually broader. It controls movement as well as the expression of emotions. It also plays a key role in the creation of the comprehensive saliency map. This is the map the cognitive processes of the frontal lobe rely upon for information about the environment (both internal and external) of the animal. The TRN is under the overriding operational control of the frontal lobe in humans. However, it operates routinely from preprogrammed instructions.

Activities related to steps 14 through 18 are shown in greater detail in the next figure. In both figures, the significant number of supervisory signal paths between the frontal lobe and the other areas of the brain are omitted for clarity. These supervisory signals are discussed within the text of this Chapter.

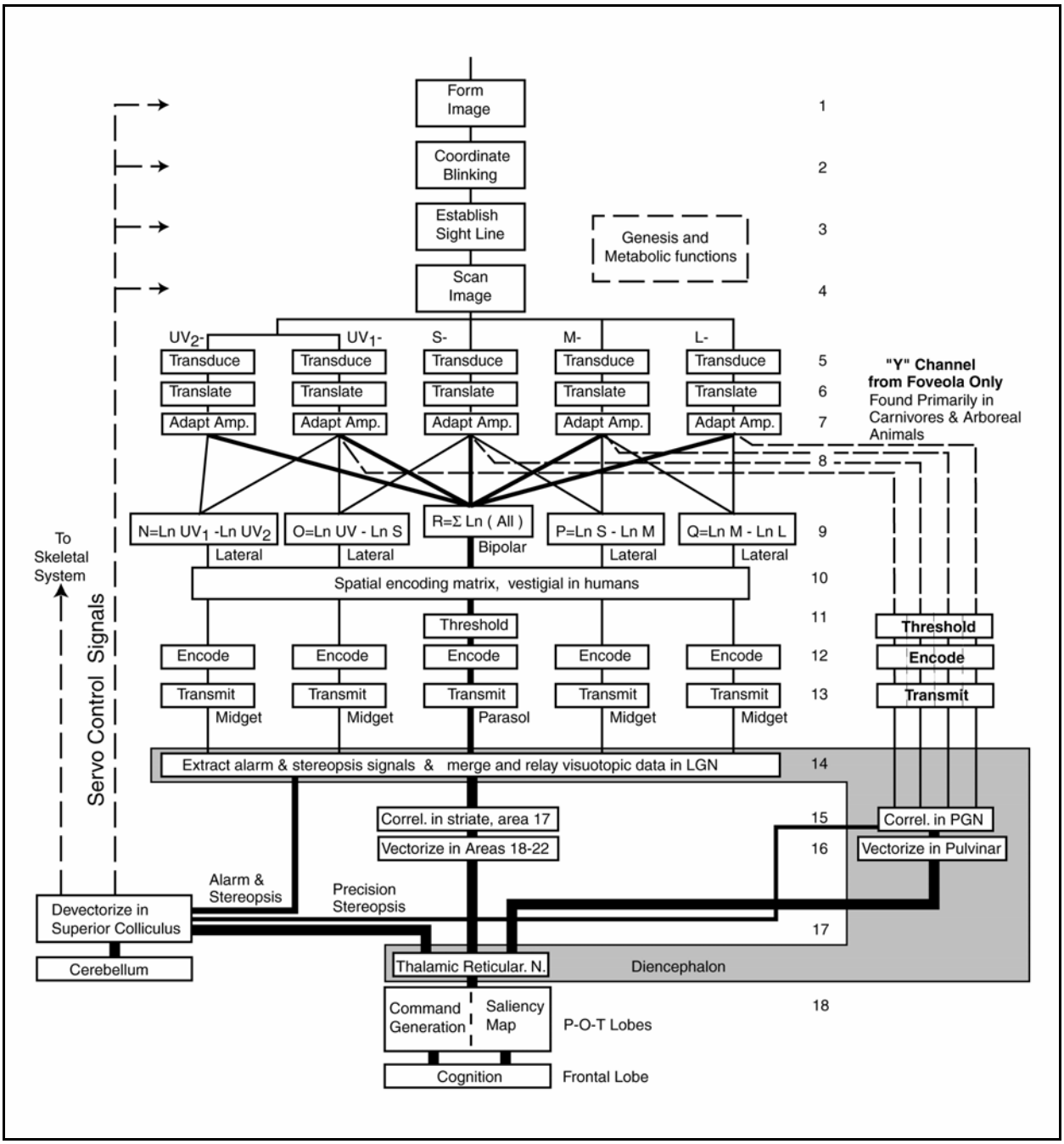

Figure 15.6.4-5 Emerging Top Level Block Diagram of vision, ca 2002. The figure details the analytical mode of vision found primarily in the carnivores and arboreal animals. It also shows the critical role played by the thalamic reticular nucleus. The role of the elements of the diencephalon, other than the LGN, are largely unreported in the vision literature. Thin solid lines represent afferent signal paths that exhibit a visuotopic relationship with the field of view. The dashed lines represent efferent signal paths. The broader solid lines below step 14 represent abstract signals in a machine language (neural code) that is unknown at present. See text.

Figure 15.6.4-6 provides a 2002 revision to [**Figure 15.2.3-5**] recognizing the large number of neural paths returning from the occipital lobe to the thalamus and showing the crucial role of the recently defined thalamic reticular nucleus. It is proposed that the signals from the LGN go to areas 17-18 and then return to the thalamic region (via the geniculo-calcerine pathway). They necessarily pass through the TRN. They are then projected along the pulvinar pathway, as interps extracted by the striate/$V_{>2}$ couple, to the parietal lobe of the brain.

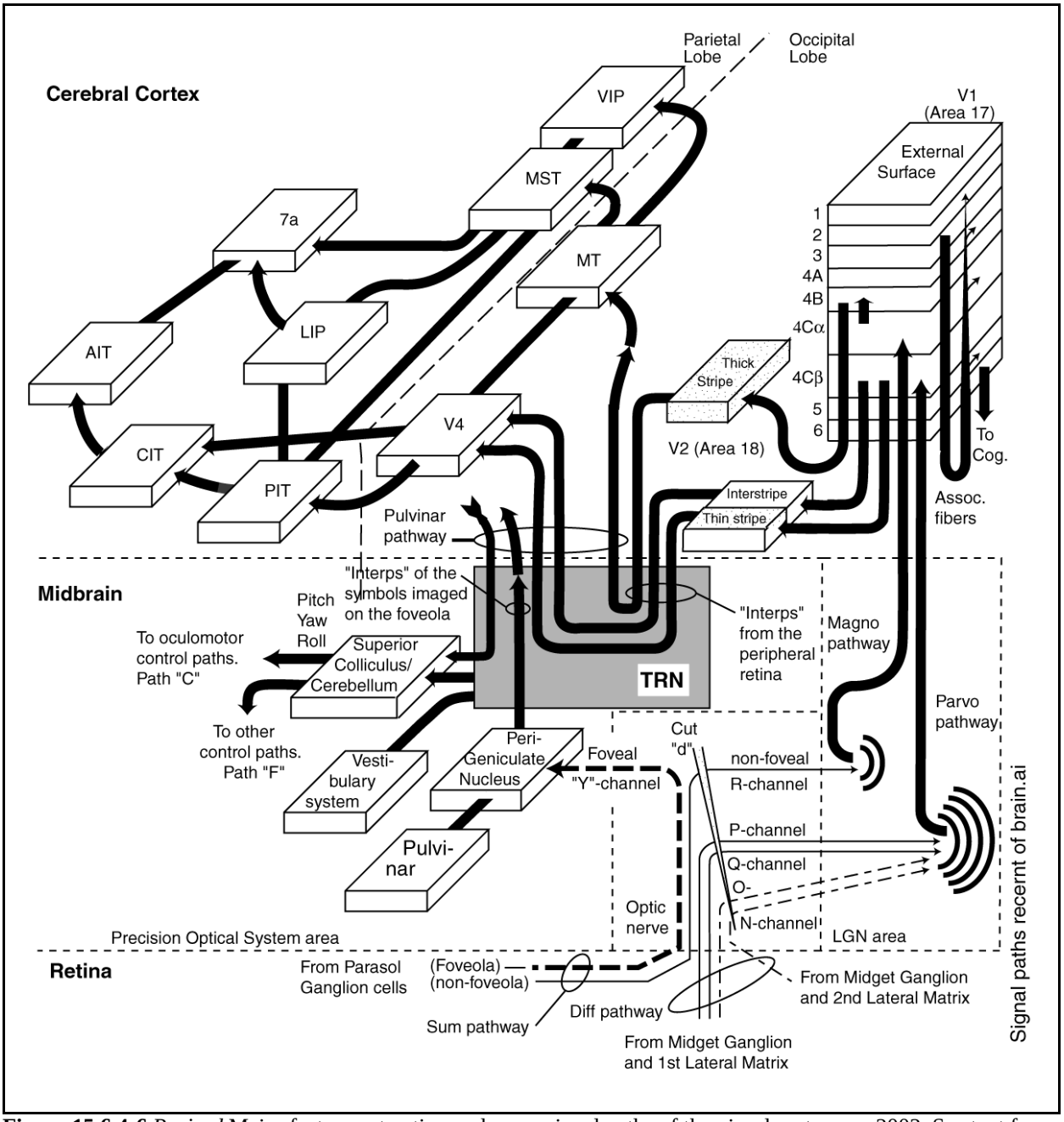

Figure 15.6.4-6 *Revised* Major feature extraction and servo signal paths of the visual system, ca 2002. See text for extensive discussion.

The figure also introduces a command signal path from the cerebral cortex (pre-motor area) back along the pulvinar pathway, through the TRN, to the superior colliculus/cerebellum couple. The rest of the discussion regarding this

figure remains the same as in **Section 15.2.3.5**.

In this representation, the signals projected to V4 and the rest of the parietal and anterior lobes are abstract. They do not contain a significant retinotopic component and small areas exhibit no field sign. This may be counter to many readers training. However, it is extensively explored in Tootell, & Hadjikhani using fMRI techniques[106].

15.6.4.5 Revision of the Functional Diagram of vision, ca 2002

Based on the work in **Section 15.6.1** through **15.6.4** and previewing some material in **Section 15.6.5** and **15.6.6**, **Figure 15.6.4-7** presents a new ly revised Functional Diagram of human vision. The first order signal (FO) paths, for both the auditory and visual modalities, of Sherman & Guillery are shown as wide hollow lines.

This new version also introduces a point of laceration of the corpus callosum (dashed line) that allows comparison of this diagram with the observed performance following "total commissurotomy," as discussed in Trevarthen & Sperry (**Section 15.6.4.5.4**).

While a long and detailed discussion of this figure could be provided, it would be largely redundant with the material already presented in **Section 15.6**. Only a few highlights will be provided below.

[106]Tootell, R. & Hadjikhani, N. (2001) Where is 'Dorsal V4' in human visual cortex? Retinotopic, topographic and functional evidence *Cerebral Cortex* vol 11, pp 298-311

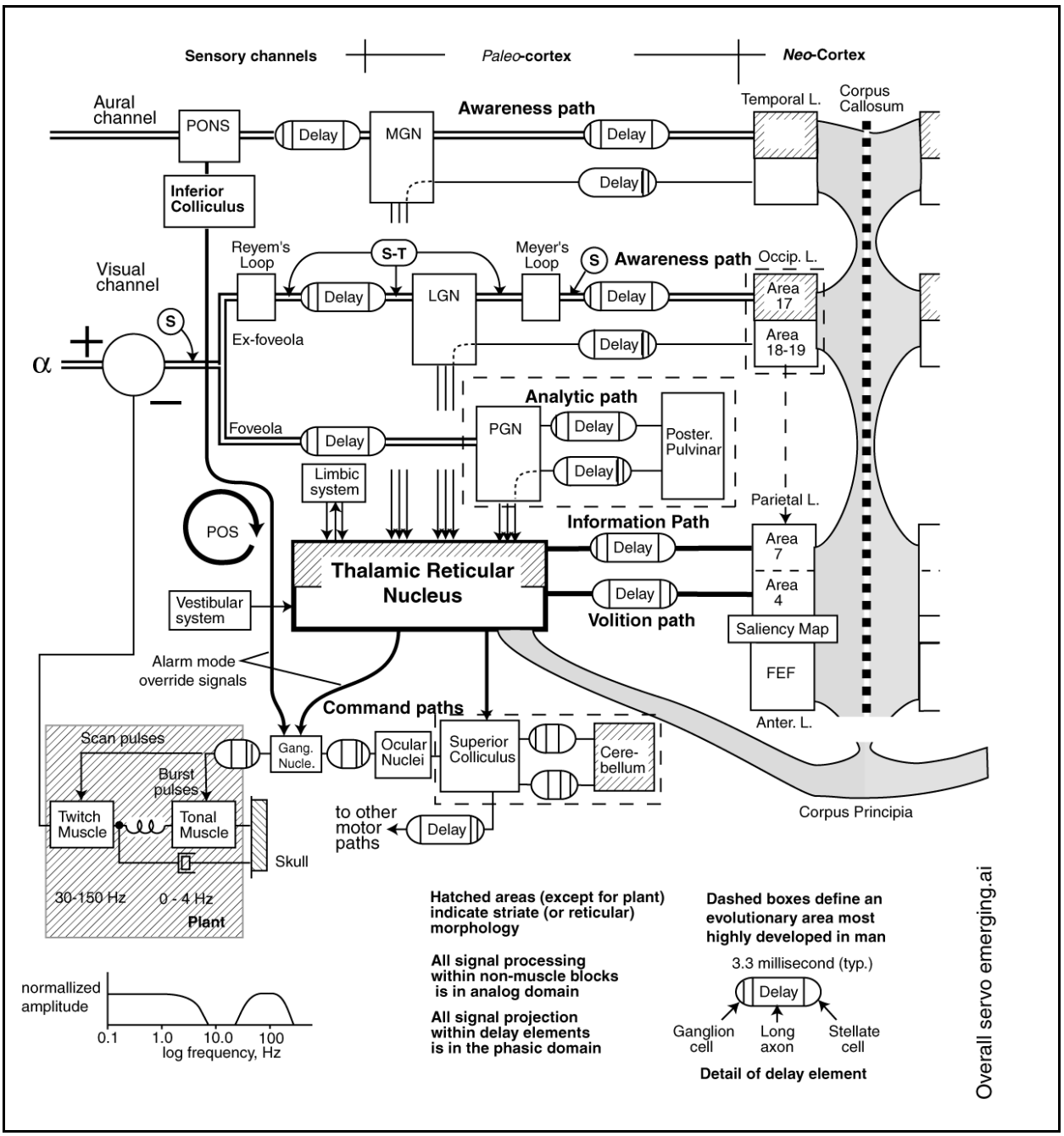

Figure 15.6.4-7 A revised Functional Diagram of human vision, ca 2002, introducing the TRN, in its role as the central control point of vision, and the relationship between the left and right hemispheres of the cortex.. The diagram shows the nominal resolution signal path via the LGN to the striate/$V_{>2}$ couple and the high resolution signal path from the foveola to the PGN/pulvinar couple. The diagram is compatible with dual mechanisms of depth perception and shows only abstract command signals being transmitted to the SC/cerebellum for implementation. It also shows two distinct major commissure between the left and right portions of the brain. See text.

15.6.4.5.1 Confluence of signals of the sensory systems EDIT

Both Desimone & Gross and Maunsell & Newsome have contributed to the perceptual functions involving the merging of information from the individual sensory systems. Much of this merging appears to occur in the IT as labeled by Desimone & Gross or areas 7 using the more familiar notation. Maunsell & Newsome remark (page 392) on the likely presence of a mechanism associated with area 7a that causes the visual world to be presented in a stable, head-centered coordinate system. It is proposed here that the actual coordinate system employed in the higher perceptual processes (anterior to V4) is actually a head centered, earth oriented inertial coordinate system with contributions from the vestibular system. It is likely that the signals delivered to the anterior cortex via the pulvinar pathway have already been stabilized in this manner following their extraction from the Precision Optical System servo loop.

Jones and Powell provided some interesting insights concerning the merging of sensory signals in the cortex[107]. Their summary includes several pertinent conclusions. Without a precise definition of their use of the term afferent, reconciling their following comment is difficult; "only the somatic sensory areas, . . . receive an afferent cortical input." They note the loss in topographical correlation as the sensory information converges toward the central sulcus, CS, in their terminology, and the beginning of sensory signal assimilation as the topographical correlation is lost.

15.6.4.5.2 Agnosia as a function of location or feature extraction engine EDIT

Kandel, Schwartz & Jessell[108] have provided a table of visual agnosia by area of cortical lesion. Unfortunately it is dated 1980 and it can be assumed that better data is becoming available almost daily. Their synopsis concerning the blind painter on pp. 586-587 is important and touching. Discussions of this author with a clinical patient have also suggested the results of agnosia in the vicinity of area 7. Thee discussions concerned the merging of the vector data (abstract signals) from the PGN/pulvinar couple (related to the foveola of the retina) and the vector data received from the striate/$V_{>2}$ couple (related to the non-foveola retina). He reported a shimmering area consisting of a wheel with a diameter of about 2-3 degrees and five or six equally spaced spokes radiating from the wheel. Whether these features were directly associated with the conformal transformation presented at the striate cortex could not be determined. However, the number of spokes and possible damage involving the low resolution image of the fovea, found in the striate cortex, could explain these symptoms.

Global anterograde amnesia is discussed in Steriade, et. al[109]. With this condition, the subject is no longer able to recognize people, places, facts etc. It is frequently associated with problems in either the thalamus or the parietal lobe of the *neo*-cortex.

15.6.4.5.3 Effect of a "total commissurotomy" of the corpus callosum

Trevarthen & Sperry reported the results of complete commissurotomies on a number of their patients up through 1973[110]. Their report was presented based on the conventional wisdom of that time. That wisdom assumed the only signaling path between the two sides of the cerebral hemispheres was via the corpus callosum. They noted the observed performance of their patients was not compatible with this framework. However, the performance is compatible with the Top Level Schematic presented above. Their patients performance highlights two situations. There is clearly a path between the two halves of the cerebral hemispheres independent of the corpus callosum which was not interrupted surgically. This path is the corpus principia, a portion of the internal capsule connecting the two halves of the thalamus, and the two halves of the TRN. While not as large as the corpus callosum, it is clearly as important or more important. There may also be additional paths passing from one side to the other within the bulk of the thalamus. These paths were only discussed in concept in Trevanthen & Sperry.

The subjects were asked to report their visual capability using their voice. Since the vocal system is a motor system controlled by the TRN and commanded by the SC/cerebellum couple, a patient will be able to report an alarm signal received from either of the cerebral hemispheres without relying upon the corpus callosum.

The main role of the corpus callosum in vision appears to be to aid in the merging of the images from the left and

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[107]Jones, E. & Powell, T. (1970) An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. Brain, vol. 93, pp. 793-820

[108]Kandel, E. Schwartz, J. & Jessell, T. (2000) Op. Cit. pg. 498-500

[109]Steriade, M. Jones, E. & McCormick, D. (1997) Op. Cit. pg 689

[110]Trevarthen, C. & Sperry, R. (1973) Perceptual unity of the ambient visual field in human commissurotomy patients. *Brain*, vol. 96, pp 547-570

right halves of the visual field. With training, a subject may regain nearly normal visual facility after a complete commissurotomy, except for the ability to merge images that cross the medial line dividing his visual field vertically.

Based on the 2002 model of this work, a total commissurotomy is probably not an appropriate name for the procedure of Trevarthen & Sperry. It would be better to speak of a total corpus callosumotomy.

The emerging model provides a more comprehensive explanation for the performance of the subjects of Trevarthen & Sperry both before and following their operation. The medical implications are discussed briefly in **Section 18.8.6**.

15.6.4.5.4 Visual task assignments based on the emerging figures of Section 15.6.4

Recent empirical and theoretical work has demonstrated clearly that the so-called "primary visual cortex" is not a primary element of the visual system. While physically easy to investigate, its importance is eclipsed by the diencephalon, with particular emphasis on the perigeniculate nucleus/pulvinar couple in humans. Furthermore, it is the shroud enclosing much of the thalamus, the thalamic reticular nucleus, that is the primary operational center of the nervous system. The typical chordate can survive and see adequately with the primary visual cortex completely destroyed or removed. The typical chordate can survive with the frontal lobes destroyed or removed. However, significant damage to the TRN leads quickly to the death of the organism. In this context, severing the corpus principia, within the diencephalon, is considerably more serious than severing the corpus callosum between the two lobes of the cerebral cortex.

Within the context of the TRN as the most important element of the nervous system, it is possible to describe the roles of the subservient elements more clearly. The TRN receives, supervises and processes signals from all of the sensory systems. The location of many neural engines is determined by their operational importance and the time delay involved in transmitting and receiving information between them and the TRN. Time delay, related to the propagation of stage 3 (phasic) signals within the neural system, is a very important parameter of many signaling paths. In this context, the PGN/pulvinar couple is much more important than the striate/$V_{>2}$ couple because of its role within the POS servomechanism. In addition, it appears a special neural complex, the ganglia nucleus along the oculomotor neural path appears to exist specifically to minimize time delay when necessary to respond quickly to alarm signals endangering the organism.. Coarse signals from the TRN to the oculomotor muscles can bypass the SC/cerebellum couple and the other nuclei associated with the oculomotor neural paths when a crisis arises.

In humans, the visual system is highly redundant. The critical aspects of the image forming physiological optics are duplicated in the two eyes. The retina of each eye consists of four sets of photoreceptors. It normally operates without the UV sensitive photoreceptors being operational because evolution has yet to discard them. The signals from the remaining three sets of photoreceptors are multiplexed in several ways. Those from the general retina are multiplexed into separate luminance and (2) chrominance channels. These signals are extended and processed in tandem as far as the striated area of the occipital lobe (area 17) of the cerebral cortex. These signals are used in the awareness mode of chordate vision. Simultaneously, the subset of the photoreceptors forming the foveola are processed in a separate channel, generally defined historically as the Y-channel in cats, at a higher resolution and in conjunction with the POS. It is these signal paths and signals that comprise the analytical mode of (at least) mammalian vision. While the awareness mode signals are not processed synchronously when they reach area 17, the analytical mode signals are processed synchronously within the loop of the POS servomechanism.

While the striate/$V_{>2}$ couple extracts information from the peripheral retina describing the external environment of the organism, the information is of relatively coarse resolution. The precise information is extracted from near the point of fixation by the PGN/pulvinar couple. Both couples return a majority of their information to the TRN, in abstract (non-visuotopic) form, for subsequent transmission to area 7 of the parietal lobe in the form of messages compatible with the saliency map. This map is maintained within the P-O-T area of the cerebral cortex and made available to the higher cognitive processing engines within the anterior lobe. These engines create instructions that are returned to the TRN via the P-O-T area, primarily via area 6. The TRN routinely routes these abstract volition commands to the superior colliculus/cerebellum couple for decoding, elaboration and implementation. The TRN operates semi-autonomously based on prior learning and stored instructions from the engines of the anterior lobe. However, it has great flexibility and can often reroute signals when necessary (or learn new methods of operation).

The lateral geniculate nuclei perform as more than relays. They are responsible for generating alarm mode signals at the earliest possible time (the primary reason the LGN's are located within the diencephalon). These signals are used by the TRN to control blinking and other reflexive actions. The LGN's also provide a coarse stereoptic error signal to the POS. A more precise stereoptic signal appears to be provided to the POS by the PGN/pulvinar couple. The superior colliculus/cerebellum couple serves to convert all of the abstract volition and alarm signals processed through the TRN into action commands that the oculomotor and skeletal motor systems can accept. It does this for

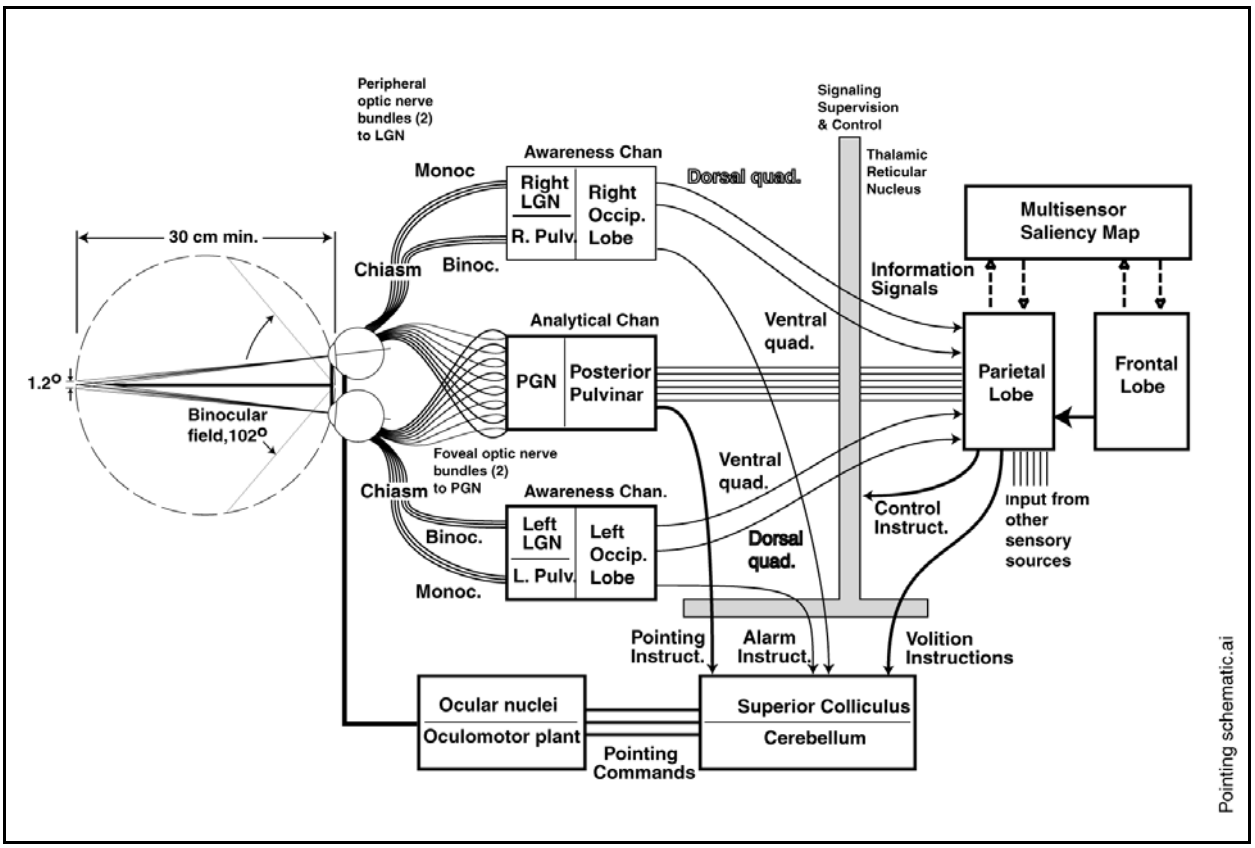

Figure 15.6.4-8 A simplified Functional Diagram of human vision, ca 2003, showing the TRN, in its role as the central control point of vision, and the relationship between the left and right hemispheres of the cortex.. The many delay elements in the system are not shown. An expanded role for the pulvinar is shown.

all of the efferent neural signals regardless of the originating sensor modality. While neurons can be located in the superior colliculus/cerebellum couple that exhibit a receptive field in object space of vision, the relationship is not one-to-one. All of the signals have passed through an abstract phase before reaching this couple.

Figure 15.6.4-8 summarizes the above discussion without showing all of the delay elements in the system. It also shows an expanded responsibility for the left and right lateral pulvinars in support of the left and right lateral geniculate nuclei. If appropriate, this modification would redistribute the memory function within the awarenss channels and further limit the role of the occipital lobe.

To achieve the performance required, the oculomotor plant is of two-stage design. The tonal portion of the oculomotor muscles responds to the majority of signals calling for saccades . However, in the more advanced chordates, the twitch portion of the oculomotor muscles respond to higher frequency commands and create the tremor motion required to achieve fine detail analysis and reading. The stage 3 (phasic signaling) neural circuits associated with tremor, including the "Y-channel" circuits of the retina exhibit a significantly higher maximum frequency than do most sensory or efferent neural channels. The top frequency appears to be near 150 Hz. Within the POS, and particularly within the PGN/pulvinar, there appear to be electrotonic signal processing circuits operating at significantly higher maximum frequencies. Some of the stage 3 circuits in this area have been shown capable of propagating signals approaching 500 Hz.

While the signaling code used in the eye and optic nerve are well understood, the machine language (neural code) used within the CNS is unknown at this time. It will be difficult to decode because it appears many of the messages are transmitted in "word serial/bit parallel format." Each word is transmitted using multiple bits that are transmitted over separate parallel neural paths. This method results in the very complex "burst patterns" reported on individual neural paths in current research. To even capture these words requires more sophisticated electronic data recording than usually used in research until about 2005.

15.6.5 Important topological features of other *couples* related to vision

15.6.5.1 The potential LGN/pulvinar *couple*

Recent analyses have hinted that the LGN's (possibly in consort with the respective lateral portions of the pulvinar) may operate in a low resolution role very similar to that of the PGN/pulvinar couple. This couple could provide low level interps of images projected onto the peripheral retinas and possibly percepts related to these images as well. If true, the LGN/pulvinar couple could provide more timely information to the parietal lobe for insertion into the saliency map. If true, the occipital lobe would function much like the cerebellum does in support of the PGN/pulvinar couple. It would provide the additional memory needed to support perception of less frequently encountered imagery.

15.6.5.1.1 Retinotopic arrays within the LGN's

The lateral geniculate nuclei of the thalamus play two major roles. One role relates to the alarm mode of operation. It is critical to the survival of the organism. The second role is to merge the information corresponding to the same visual fields from the two eyes, as a task associated with the awareness mode of vison. It then passes the merged information along to the striate cortex.

The first of these roles is primarily involved in change detection. The goal is to detect any change, in either intensity or position, within the total field of view of the eyes. Once detected, the change is passed immediately to the thalamic reticular nucleus for evaluation and action. If deemed important, the TRN will override the current activity of the POS, in order to bring the line of fixation of the eyes in alignment with the object causing the change, and cause the analytical mode to interpret the object.

The second role is involved in preliminary data reduction prior to serious data reduction within the cerebrum. The merging is accomplished with respect to the luminance, each of the chrominance channels and potentially the polarization and similar auxiliary channels. To perform this role, the LGN's create essentially complete retinotopic maps of their respective fields of view. The phenomenon of "macular sparing," actually the separation between the awareness processing channel and the analytical processing channel associated with the foveola, suggests the LGN's do not map the area of the foveola. This area is generally located near the edge of the maps as determined by electrophysiology. It may in fact not be represented in these maps. Instead, the foveola signals are mapped onto the perigeniculate nucleus, (a portion) of the TRN.

To achieve the merging of the two fields of view, it is necessary that the two retinotopic maps be brought into adequate alignment. Thus, before merging the images, the LGN's must extract an error signal describing the error in vergence associated with the images. This error signal is transmitted to the TRN for passing to the POS. It is the responsibility of the POS to eliminate any vergence error. There is a question as to whether the LGN's can provide an error signal of adequate precision to serve the needs of the perigeniculate nucleus. It performs a similar merging of the higher resolution data from the foveola. It is quite possible that the LGN's provide a coarse vergence error signal and that the PGN's provide a fine vergence error signal to the POS servomechanism. Note that the vergence error signals are averaged values. The LGN's and PGN's continue to maintain a differential error signal between individual objects in the scene. These signals are incorporated into the vectors incorporated into the relevant saliency maps. These differential signals are used to describe the depth of the object in the field relative to the average field.

Once the vergence errors have been eliminated, the merging process is basically one of summing the data, on a pixel by pixel basis from the two eyes. The individual channels remain identifiable after this process. The merged data is re-encoded into separate channels and sent over stage 3 circuits to area 17 of the occipital lobe for further processing.

The topography of the LGN's have been extensively studied in monkeys. **Figure 15.6.5-1** shows the gross topography for the monkey[111]. Six clearly discernable layers are readily seen in this figure. Hubel notes the LGN is folded along a fore-and-aft axis. The image is of a slice parallel to the face of the subject. Hubel says "the two left half-retinal surfaces project to one sextuple plate." The internal organization of these plates is still a subject of discussion. On morphological grounds, the bottom two layers are called the magnocellular layers (they contain larger cells). The upper four layers are called the parvocellular layers. The signals from each eye go to various layers in an unexpected sequence. In this left LGN, the sequence from top down is left, right, left, right, right left. He indicates the layers are faithful retinotopic maps but does not go into a discussion of precision. The number of layers in the monkey LGN suggest that the awareness channel (peripheral vision) of that species does not respond to

[111]Hubel, D. (1988) Eye, Brain, and Vision. NY: W. H. Freeman, pg 64

ultraviolet light (there is no sign of layers of unknown purpose or associated with the O-channel of biological vision).

More recent work has been reported showing an eight-layer LGN in monkeys, **Section 11.7.1.1.1**. Gray's anatomy, 40th Edition also suggests more than six layers in human LGN's[112]. "Most ventrally an additional superficial, or S, lamina is recognized."

Hubel gives the number of cells in each LGN of monkey as 1.5 million. Hubel describes, in detail, the fact that most cells in the visual cortex are only sensitive to changes in stimulus. He did not address tremor as a source of stimulus but concentrated on temporal changes. He also describes, in detail, the edge detection properties of the visual system and the fact that the response from photoreceptors illuminated by a constant intensity field do not respond at all.

Hubel provided no discussion of the difference between the LGN's of man and monkey. And, it is always difficult to rely upon one slice through a neural structure because of their variation in shape with position. The figure does not show any structure, such as a thalamic reticular nucleus, surrounding the LGN. Nor does it show any perigeniculate nucleus adjacent to it. It is possible that he selected this image for its pedagogical value as opposed to its total description of this general area of the thalamus. Other authors show less symmetrical cross-sections[113]. The views in figures 6.32 through 6.34 of Steriade, et. al. are particularly enlightening in this respect, as is the extensive discussion and references in that chapter. Their figure 6.34 shows the spatial map of the individual layers in the monkey. It is important to note that the line of fixation occurs at the very edge of each surface of the LGN (if it is represented on the surface at all). Essentially no area is available to process the considerable number of photoreceptor signals available from within a nominal one degree diameter foveola. This condition would suggest the presence of a separate perigeniculate nucleus serving the foveola in monkey.

Figure 15.6.5-1 Gross topography of the left LGN of a monkey. The dashed line represents a sagittal plane. Six individual layers show clearly. Each layer contains neurons (dots) in four to ten or more discernable sublayers. From Hubel, 1988.

Figure 16-7 in Nolte (1999) shows the human LGN capped over a large area by part of the thalamic reticular nucleus. The commissure of the internal capsule are on the other side of the TRN. The scale of the figure does not allow identification of individual layers within the LGN. It is proposed that this difference between the human and monkey thalamus (and its components) is a significant difference that separates the visual and cognitive capabilities of the two species. While the availability of data from monkeys (particularly un-anesthetized monkeys) is precious with regard to the awareness mode of vision, it is of negligible value in understanding the analytical mode of human vision.

The next paragraph will provide a caricature of the human LGN & the PGN portion of the TRN. It also includes a discussion accompanying this [**Figure 15.6.5-2**]. It will be noted here that the vergence error, ψ, is almost certainly computed from the luminance channel data, the magnocellular layers, because these layers receive much wider bandwidth (more time responsive) signals than do the parvocellular layers.

15.6.5.2 The LGN/occipital couple

The most obvious couple of the visual modality based on histology and anatomy is the LGN/occipital lobe couple.

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[112]Standring, S. ed. (2008) Gray's Anatomy, 40th Ed. NY: Elsevier pg 314

[113]Steriade, M. Jones, E. & McCormick, D. (1997) Thalamus, vol. 1. NY: Elsevier. Chapter 6

The terminology may be a bit informal based on recent information. Whereas the LGN was previously thought of as primarily a relay point, it is now recognized as the primary engine supporting binocular vision, individual figure specification within the cyclopean field of view delivered to the occipital lobe for additional analysis. The feature of this couple not yet fully appreciated is the very large number of backprojection neurons from the occipital lobe to the "LGN." It is highly likely that these backprojection neurons will be found to involve multiple neuron groups (commissure) supporting word serial/bit parallel projection of extracted information back to the TRN (a covering of the LGN) for subsequent switching and forwarding, rather than to the LGN. The number of backprojection neurons have been estimated as up to 30 times the number of forward projecting neurons from the LGN. [xxx find and add citation]

Many of the backprojection neurons may not emanate from area 17, V1. They may emanate from other portions of the occipital lobe as suggested in the next paragraph..

As frequently noted in this work, the LGN/occipital couple, and more specifically the occipital lobe of the brain does not participate in the extraction of fine detail from the visual field. This Analytical Mode activity is principally performed via the PGN/pulvinar couple. The man-made circuit techniques attempting to perform information extraction are discussed in **Section 19.10.5** of this work.

15.6.5.3 The striate/$V_{>2}$ *couple* EDIT

[xxx occipital lobe splits into striate and prestriate (non-striate)]
Jain, et. al. have shown the terminal locations of various commissure between the LGN and the posterior occipital lobe of cats and several prosimians based on staining[114].

Conley & Diamond have described the primary signal paths related to the striate/$V_{>2}$ couple. It appears the afferent signals originate primarily in the LGN and terminate in area 17 while the efferent signals originate in areas 18 and higher and terminate in the pulvinar.

Glaser says only about one third of the striate cortex is on the surface of the occipital lobe[115]. The major portion of it lies buried in the calcarine fissure, its branches, and accessory sulci. His description continues.

15.6.5.3.1 The emerging architecture of the occipital & posterior parietal cortex

Understanding of the signal architecture of the visual system up to location V1and into V2-V3 is progressing rapidly. Beyond this location, the literature is less than complete and the signal architecture can only be estimated based on very limited information about the number and purpose of feature extraction engines in the perceptual subsystem. At this time, the organization of the cognitive subsystem is almost completely unknown. Several psychologists have proposed models of the cognitive subsystem but these are extremely general and cannot be tested at this time using the scientific method. Treisman & Gormican have suggested a model of the "attention" mechanism based on a simple pyramid architecture[116].

The understanding of the operation of the higher level perceptual areas anterior to areas V2 and V3 is also moving forward based on different criteria than for the posterior areas. Up to area V4, there appears to be at least a coarse topographical correlation between the retina and the surface of the cortex. Anterior to these areas, any such correlation is minor or entirely lost. As noted by Desimone & Gross[117], in these anterior areas, the area immediately around the point of fixation (they use the expression "center of gaze") dominates the individual feature extraction engines. This is strong corroboration that it is the signals from the foveola that are the primary source of signals in perception. Their summary stresses the lack of spatial correlation of the areas they studied in the inferior temporal cortex, IT, with the topography of the retina. Instead, they found areas that were responsive to the entire visual field but lacked a topographical relationship to that field.

They also found large areas of the cortex dorsal, anterior and ventral to the IT to contain large areas devoted to

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[114]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
[115]Glaser, J. (1999) Neuro-ophthalmology, 3rd ed. NY: Lippincott Williams & Wilkins pg 90
[116]Treisman, A. & Gormican, S. (1988) Feature analysis in early vision" evidence from search asymmetries. Psychol. Rev. Vol. 95, no. 1, pp. 15-48, figure 15
[117]Desimone, R. & Gross, C. (1979) Visual areas in the temporal cortex of the macaque. Brain Res., vol. 178, pp. 363-380

polysensory processing. The lack of topographical mapping and the polysensory nature of the signal manipulation strongly implies that the areas anterior to V4 are focused on higher level perception and probably the initial stages of command assimilation.

Desimone & Gross are careful to define the nature of the signals they recorded. They stress the size of their probes versus the size of neurons. They made special efforts to record the activity of individual neurons on occasion but normally recorded "multi-unit activity." This activity usually involved multiple action potentials imposed on an unresolved background. It is not clear that they were able to differentiate between efferent and afferent neurons at the sites probed. They also characterized their stimuli, many of which were highly structured. They employed an unfolded map of the cortex that was not provided in the paper, although some parts of it were. Their results indicated that 98% of the receptive fields measured included the point of fixation and that the large majority of the receptive fields included the merged visual field of both eyes. To be sure their results were not coincidental baed on their multi-unit method of recording, they performed similar measurements by recording signals from individual neurons. They plotted 219 fields and found that all but five units had receptive fields that included the point of fixation and that usually the greatest response was to stimuli presented at the point of fixation.

Friedman-Hill et al. have recently provided some interesting material based on bilateral lesions of the posterior parietal lobe in one patient[118]. The work suggests a disconnect in the visual portion of his saliency map.

15.6.5.3.2 Functions of the inferior temporal cortex

Desimone & Gross summarized their work by saying: "the inferior temporal cortex may contain the 'highest' or 'ultimate' visual pattern processing mechanisms." They listed six reasons for this conclusion:

1. Removal of this area produces more complex visual deficits than the removal of any other visual area.

2. It is the greatest distance, path-length-wise. from the retina of any area solely responsive to visual stimuli.

3. The IT receives converging signals from topographically organized areas of the prestriate cortex.

4. IT neurons often have particularly specific and complex trigger features.

5. The visual response of the IT are modulated by the animals state of attention as well as the significance of the stimuli.

6. Unlike other visual neurons, IT neurons have large receptive fields, often bilateral, within which the optimal stimulus is optimal throughout the field.

They say the properties of the IT cortex are qualitatively different from those of the prestriate visual areas.

15.6.5.3.3 Signal paths and time delays within the occipital cortex

Although the discussion during the 1980's focused on the ubiquity of a dichotomy, the discussions were not exclusionary and sometimes harbored apparent internal inconsistencies. These were sometimes due to inadequate definitions. Maunsell & Newsome[119] developed the concept of two major pathways in visual processing based on a motion pathway and a separate color and form pathway. However, their motion pathway did not correlate well with the basic parameters of the stimulus such as direction or speed. They caveat their material with the statement that "it seems unlikely that these streams are completely independent." Since the number of features actually examined and/or extracted by the cortex from the imagery forming the stimulus is unknown, it seems premature to focus on two arbitrarily defined pathways.

Re-interpreting their discussion of the motion pathway on page 379 leads to the conclusion that the cortex evaluates motion in terms of changes in object position with time and not in terms of their velocity as it relates to spatial frequency. This would appear to be more rational since no temporal frequency selective filter circuitry has ever been found within the cortex. Alternately, the computation of average velocities based on the changes in position with time is quite straight forward. The measurement of simple time delays is easily accomplished with a first order RC

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[118]Friedman-Hill, S. Robertson, L. & Treisman, A. (1995) Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions *Science* vol 269, pp 853-856

[119]Maunsell, J. & Newsome, W. (1987) Op. Cit. pg. 375-390

filter and boolean logic. It appears that area 7a is highly involved in such computations[120].

In order to maintain the dichotomy of two principle pathways, they caveat that the color and form pathway has been less intensely studied than the motion pathway. They continue, "Little is known about the color specificity of neurons in the later stages of the color and form pathway to which V4 projects." They did contribute one significant feature of cortical processing related to illusions. They commented on the work of Von der Heydt, et. al[121]. who tested the response of neurons in areas V1 and V2 of macaque. They constructed illusory imagery where a bar or line appeared to span a region that was in fact blank. They reported that the signals in V1 represented the bar as interrupted but the signals in V2 represented the bar as continuous. This would suggest that the blind spot of the retina is faithfully mapped into V1 but is replaced in V2 by a fictitious piece of imagery based on the use of a "paint program."

Based on the proposed organization of the occipital cortex based on a star network, it is suggested that there are an uncountable number of visual signal paths through the occipital cortex beginning with the three principle inputs from the S and D pathways (via the LGN), and the S' pathway (via the PGN). To specify any one or two paths as of dominant importance within the cortex probably displays the predilections of the specific author. Based on the three principle pathways enumerated above, it is proposed that the principle signal paths within the cortex begin with luminance information based on signal summation and an array of difference signals related to color, form, and polarization where appropriate, originally formatted in the retina . In all animals, there are at least two distinct chrominance channels. The number of form channels is entirely unknown. However, form appears to play a minor role in the signal manipulations of the retina of man and the primates.

If one accepts the uncountable number of paths through a star network of an unknown number of nodes (but probably larger than a dozen for just the visual system), the subject of serial versus parallel processing becomes moot. Of greater significance is the relative time delay between the outputs of the various feature extraction and command assimilation engines. These delays can significantly impact the perception of events and the effectiveness of the animals response to these events.

Since the chromatic information provided to the occipital cortex is already encoded as difference signals based on the original spectral channels, there is no obvious reason for the cortex to provide a *first order* chromatic differencing function as suggested in some of the literature. On the other hand, Zeki[122] has recorded signals that suggest the computation of *second order* chromatic differences within the cortex.

Review of the concluding comments of Maunsell and Newsome (page 393) in the context of this discussion suggests a variety of needed research initiatives.

[lost its home xxx]

> The recognition of the auxiliary summation pathway between the retina, pretectum, super colliculus and areas 5 or higher of the cortex and the fact this pathway carries the high precision foveal signals without passing through the "primary visual cortex" raises a question about the descriptor "primary." It also suggests why attempts in the 1980's to cure blindness by introducing electrodes into the "primary visual cortex." First, this area is not a reasonable topographical equivalent of the retina. Second, the signals at this location are already in a engram, or vector, form. *And third, the most important visual signaling paths, involving signals from the foveola, do not pass through this structure at all.* They appear to proceed directly to area V5. It is clearly appropriate to consider a new name for this region of the cortex known also as area 17 and/or area V1.

Pansky, et. al[123]. have provided a table of signal velocities and action potentials found within the neural system. Their discussion is limited to action potentials.

15.6.5.3.4 Theoretical topology of the striate cortex

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[120]Maunsell, J. & Newsome, W. (1987) Op. Cit. pp. 383-385

[121]Von der Heydt, R. Peterhand, I. & Baumgartner, G. (1984) Illusory contours and cortical neuron responses. Science, vol. 224, pp. 1260-1262

[122]Zeki, S. (1980) The representation of colours in the cerebral cortex *Nature*, vol. 284

[123]Pansky, B. Allen, D. & Budd, G. (1988) Op. Cit. pg 356

The topology of the striate cortex advanced very rapidly during the 1980's. Schwartz provided a range of sophisticated mathematical analyses related to the topology of the striate cortex[124]. In 1985, Schwartz and Tootell, et. al. engaged in an interesting debate[125]. Concurrently, Dow, et. al. provided precise data on the topology of the striate cortex in the area of the point of fixation using electrophysiological techniques on awake monkeys[126]. Tootell, et. al. provided a very comprehensive mapping of the striate using radiographic techniques on anesthetized monkeys[127]. In 1994, Schwartz expanded his work and compared it with that of Tootell[128]. He also called for more rigorous experimental procedures leading to the inclusion of error bars or other confidence limits in the data sets.

As a result of the above work, an understanding of how the brain extracts major features from a scene is emerging. It is becoming clear that the various blobs, puffs and other quaintly named elements are feature extraction engines with a typical diameter of one mm. The gross topology of these engines in the striate cortex appear to be directly related to the conformal mapping of object space on the striate cortex.

> A mapping of object space onto a subsequent location within the visual system is defined as a **visuotopic projection**. Many authors have used the expression retinotopic projection for the same mapping. However, a retinotopic projection only equals a visuotopic projection under the paraxial assumption applied to spatial geometry instead of the more demanding spatial resolution criteria. If investigators limit their investigations to within a few degrees of the line of fixation, the term retinotopic can be used synonymously with visuotopic. However, in the general case, it cannot be.

Nearly all of the experimental work to date has occurred within +/-10° of the line of fixation. This has led to a number of simplifications in deriving the mathematical models of the visuotopic projections. A cursory look at a projection of object space onto the surface of the striate cortex suggests one of several conformal transformations. There are three basic types of such conformal transformations;

- a variety of linear and bilinear forms,
- a variety of algebraic forms and
- a variety of exponential forms.

The literature contains only the modeling by Schwartz at present. He defines his basic assumptions in his 1980 paper describing what he called the computational anatomy leading to the projection of object space onto the striate cortex. He was also careful to define a number of specific terms, including the concept of the cortical magnification factor, CMF, as a constant times a unit vector. The most basic of his assumptions was that the empirically measured CMF's tended to be inversely proportional to the degree of eccentricity at their location. This led him to adopt the conformal transformation, $w = \log (z + a)$ where z is a complex function of the form $x + jy$. The a was required to prevent the function from failing at $z = 0$. He justified this choice by noting that this complex logarithm function is the only analytic function which maps an annulus (retina) to an (approximate) rectilinear strip. However, there are two problems with this position. First, **there are similar analytical functions** that map both an annulus and a parabolic function to a truly rectilinear strip. Second, the logarithmic form results in a symmetrical function where the two ends of the vertical meridian at infinity are mapped into a single point in w-space (his pg 648). Schwartz recognizes this shortcoming in his early papers and avoided the problem by limiting the application of the transform to a zone within +/- 10° of the point of fixation. In later papers, he introduced a second logarithmic function as a correction to account for the poor fit beyond ten degrees. However, he did not show that it was an appropriate correction. The form of this correction is addressed below.

At a more precise level, there are additional problems with the Log(z+a) transform. The empirical data, to be discussed in the next section, appears to show a discontinuity along the horizontal meridian. The Schwartz formulation does not show a discontinuity along the axis of the transform. In addition, the visuotopic (or retinotopic) space is projected as a circle, centered at "a," in the transform space of the Log(z+a) transform. The empirical data of the next section shows clearly that the striate projection is not circular.

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[124]Schwartz, E. (1980) Computational anatomy and functional architecture of striate cortex *Vision Res*. vol. 20, pp 645-669

[125]Schwartz, E. (1985) On the mathematical structure of the visuotopic mapping of *Macaque* striate cortex. Science, vol. 227, pp 1065-1066

[126]Dow, B. Vautin, R. & Bauer, R. (1985) The mapping of visual space onto foveal striate cortex in the *Macaque* monkey. *J. Neurosci*. vol. 5, no. 4, pp 890-902

[127]Tootell, R. Switkes, E. Silverman, M. & Hamilton, S. (1988) Functional anatomy of Macaque striate cortex. *J. Neurosci*. vol. 8, pp 1500-1624

[128]Schwartz, E. (1994) Computational sutdies of the spatial architecture of primate visual cortex. In Peters, A. & Rockland, K. ed. Cerebral Cortex, vol. 10, pp 359-411

Figure 15.6.5-2 provides additional background on the overall visuotopic projection to the striate cortex. The labels above the figure describe the nature of the computational anatomy found below them. Also described are the states of signal dispersion found below the labels.

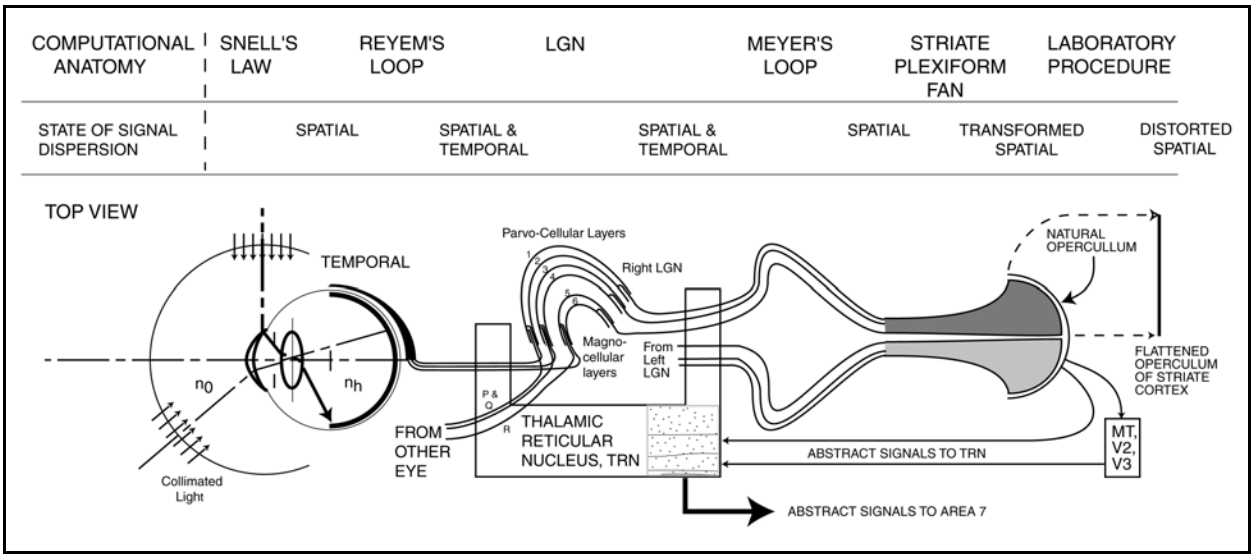

Figure 15.6.5-2 Steps in the creation of a visuotopic representation at the striate cortex. The key location of the TRN is shown. Signals pass from it through the LGN/Occipital loop and back to it. Snell's Law introduces a significant distortion between object space and the retinal map. The other major rearrangement of signals occurs in the commissure approaching the striate cortex. See text.

This figure is assembled from those developed earlier in **Sections 2.4.1, 2.6.1, 2.8.1** & **15.2.5**. The operational impact of Snell's Law is shown on the left. Because of the difference of index of refraction between air and the viscous humor of the eye, the image on the spherical retina is trigonometrically compressed as a function of distance from the fovea. Because of the finite velocity of signal projection around the circumference of the retina (a feature labeled Reyem's loop in this work), the signals that were dispersed in spatial position are also dispersed in time. The signals from the retina are rearranged within the optic nerve and optic chiasms to isolate the signals into four distinct quadrants of the visual field (plus those related to the foveola, which are treated separately). The signals are passed through the TRN where their time dispersion is used by the LGN to obtain stereopsis error signals. After passing through the TRN again, the temporal dispersion is eliminated by Meyer's loop. As the signals approach the striate cortex, they are rearranged within the geniculostriate commissure to perform a parabolic conformal transformation. This results in the superior and inferior fields related to each side of the retinas going to the appropriate operculum of the striate cortex. Finally, the operculums are flattened in the laboratory as a matter of convenience.

It can be argued that there is a spatial distortion of the signaling data between the input and the output of the LGN. However, no useful reason for such distortion has been found. The spatial rendition of the output appears to be as faithful as a "contact print" of the input. Thus, in transferring the image from object space to the striate cortex, the sources of spatial distortion are those due to Snell's Law, the conformal transformation, and any distortion due to the flattening process. The flattening process is a significant source of distortion that will be discussed below.

The conceptual requirements stated by Schwartz can be extended to recognize two additional conditions. [**Figure 15.2.3-8**] in **Section 15.2.3.7.1**, shows the mapping on the operculum is parabolic, not circular, in shape. There is likely to be, and experiment has shown, a discontinuity along the horizontal meridian of each operculum of the striate cortex.

Kober[129] has provided a parabolic transform that appears to more closely fit the physical conditions of a striate cortex (as shown in the above reference). The algebraic function $w = z^2$ projects the left or right half of a retinal map into a single parabolic sector in striate space. Radials from the point of fixation are represented by parabolic curves. These

[129]Kober, H. (1957) Op. Cit.

curves approach straight lines as they approach the horizontal, x-axis. The transform also transforms circles centered on the line of fixation, into straight lines in striate cortical space. This transform also exhibits a discontinuity along the axis of the parabolic region. Guillemin has noted (reversing the roles of *w* and *z*) the $w = (z)^{1/m}$ has a Riemann surface entirely similar in its structure to that of the function $w = \ln z$ except that the latter has an infinite number of leaves[130].

From the above, it is clear that an annulus in z-space, centered on the line of fixation projects to a truly rectilinear strip in w-space. There is no need for the factor "a" in the parabolic transform, since the function is well behaved at $z = 0$.

The transform proposed by Schwartz did not provide any asymmetry in the CMF between the superior and inferior visual fields. This became a subject in the dialog between Schwartz and Tootell, et. al. in 1985. The parabolic conformal transformation can account for such an asymmetry.

It will be shown in the next section that the parabolic conformal transformation more closely matches the computational anatomy required. This is true at least for the monkey. More laboratory investigations will be required to show it applies to humans.

15.6.5.3.5 Empirical topology of the striate cortex

The method used by the Tootell, et. al. group has provided the largest volume of test data. However, their method has not provided detailed data in the area of the point of fixation. The Dow technique, while requiring a great deal more time and effort, has provided the highest precision data near the point of fixation. Taken together, the data can be interpreted well using some of the mathematical concepts defined by Schwartz, largely independent of the specific conformal transform used. Tootell, et. al., in responding to Schwartz in the dialog, noted the variation in the curvature of the lines perpendicular to the horizontal meridian. These variations are suggestive of a second order mechanism within the projection process that is not yet identified.

Figure 15.6.5-3 shows the visuotopic data of Tootell, et. al. along with a theoretical model based on a rotated parabolic conformal transformation. The theoretical model faithfully represents the projection of the vertical meridian in object-space into a parabolic arc in striate-space, and the projection of the horizontal meridian in object space into a straight radial (a parabola of very long focus) in striate space. The circles centered on the point of fixation become nominally straight lines in striate space (with a finite concavity toward the point of fixation). It is difficult to resolve detail in the area of the point of fixation using the deoxy-glucose, DG, technique.

The lines in striate space representing circles in object space are not perfectly straight (or consistently concave toward the point of fixation) in the samples from Tootell, et. al. This can be due to second order requirements within the visual system that are not currently understood. Alternately, they can be due to the laboratory procedures used. Tootell, et. al. flattened their operculli as a matter of practical convenience. This flattening amounts to a projection in map-making. Thus, the flattened representation of a spherical surface necessarily introduces distortions. The detailed method of flattening becomes relevant. If the operculum was flattened by rolling , the resulting projection will be of the Mercator type. Such a projection can introduce curvatures into all of the lines representing great circles (straight lines) on the original surface. If the flattening was accomplished by establishing a plane tangent to the point of fixation on the original surface, and then flattening the surface with respect to that plane and fixation point, a polar projection will result. In this projection, all of the great circles on the striate cortex passing through the point of fixation will become straight lines in the projection. Future experimenters should consider the latter approach. The slight deviations in the curvature of some of the lines in Tootell, et. al. appear to be due to their flattening technique.

In 1994, Schwartz introduced a wire frame model of the operculum and used computer techniques to flatten the operculum under a set of minimum distortion conditions. It appears this technique can avoid some of the distortions mentioned in the previous paragraph. However, the set of conditions used need to be documented.

The blind spot of the eye should have a significant presence in projections of this type. Since the images of the two eyes are merged at the striate cortex, differential stimulation of the eyes should surface this feature. However, it occurs two degrees above the horizontal meridian and 16 degrees from the vertical meridian, relative to the point of fixation in object space in humans. The representation of the blind spot may be located deep in a sulcus. Kennedy, et. al. have recorded this differential effect in monkey[131]. They note the blind spot is represented by an elongated

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[130]Guillemin, E. (1956) The Mathematics of Circuit Analysis, 4th printing. NY: John Wiley & Sons pg 317

[131]Kennedy, C. (1975) Mapping of functional neural pathways by autoradiograpic survey of local metabolic rate with [14C] deoxyglucose *Science*, pp 850-853

area of 3.4 mm from front to back. This elongation of a small, horizontally displaced, circle in object space is compatible with the proposed parabolic conformal transformation. It would be represented by the horizontal axis to the right of the focus in the striate projection. This elongation is not shown in the wire frame model of Schwartz ('94, fg 14).

It is interesting that Tootell, et. al[132]. quote Van Essen, et. al[133]. to the effect that "[DG mapping] is inherently more precise than physiological methods. . ." in the light of the significantly more precise physiological data of Dow presented in the same time period. Dow does admit the physiological method is more time consuming.

Tootell, et. al. experimented with both equally spaced and logarithmically spaced concentric circles in object space. The parabolic conformal transformation would suggest an inverse sinusoidal spacing would give truly equal spacing in striate space. The small difference between the logarithmic and inverse sinusoidal spacings may be hard to document in the laboratory, unless the more peripheral retina is involved.

[132]Tootell, R. Switkes, E. Silverman, M & Hamilton, S. (1988) Op. Cit. pg 1531

[133]Van Essen, D. Newsome, W. & Maunsell, J. (1984) The visual field representation in striate cortex of the macaque monkey. Vision Res. vol. 24, pp 429-448

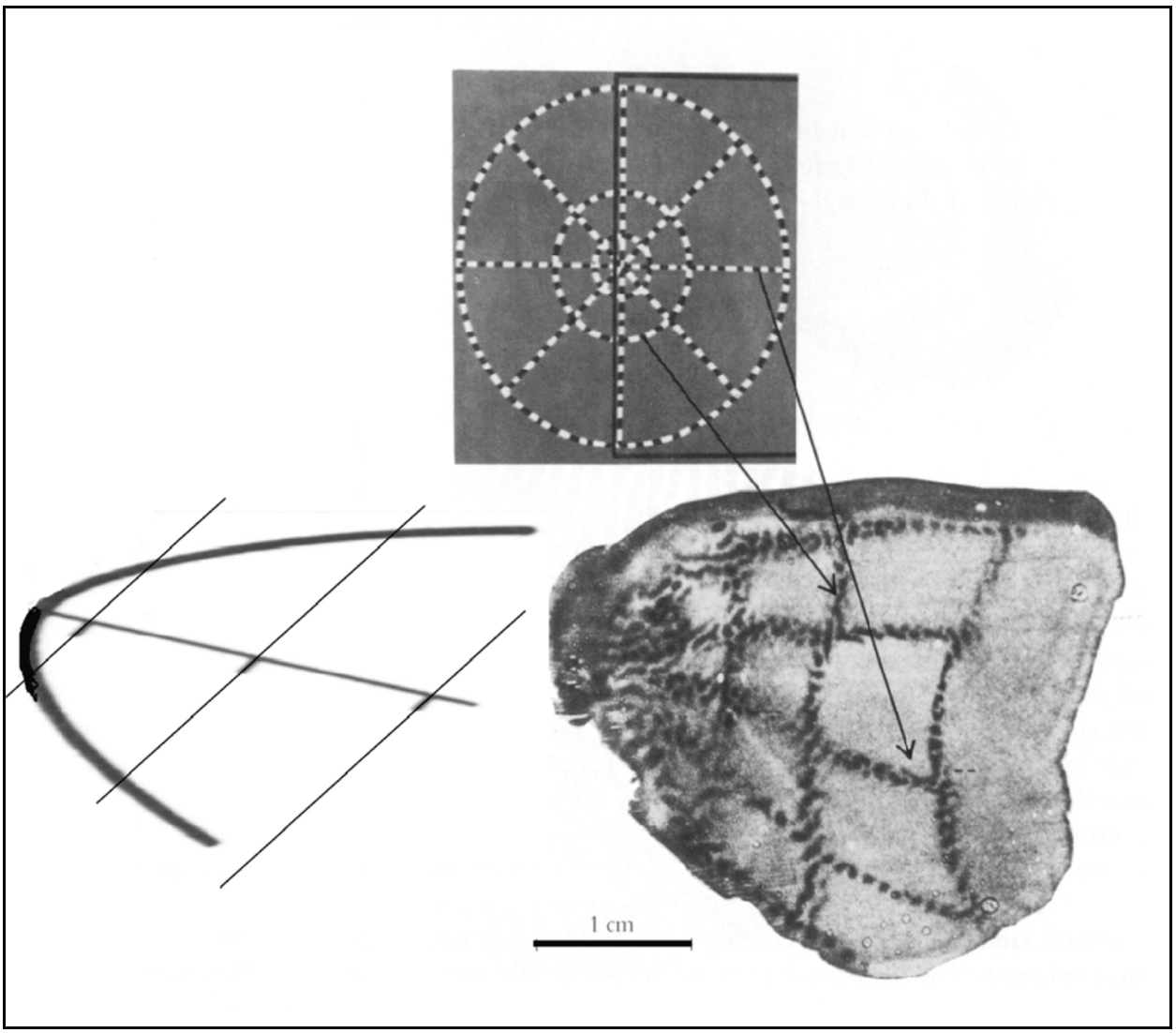

Figure 15.6.5-3 Visuotopic projection of right half of object plane onto one operculum of Macaque striate cortex. Top; image with three circles at 1°, 2.3° & 5.4°. Note, left edge of mask is to the left of the point of fixation and vertical meridian. Right; image recorded using DG technique. Left; theoretical projection of vertical meridian (curved line) and horizontal meridian (straight line) based on rotated parabolic conformal transformation. Top & Right from Tootell, et. al., 1988.

Figure 15.6.5-4 shows another view from Tootell, et. al. and the rotated parabolic transform. The transform was computed using a generic equation that required the focus of the parabola to be at the origin of the coordinate system. This equation prevented the width of the parabola from being changed in the caricature. The caricature highlights the discontinuity along the horizontal meridian in object space. Subject to the above comments about flattening, it would suggest the dashed axis on the right should be a straight line. The stars indicate the point of fixation in both frames. The vertical meridian, transformed into a parabola, is drawn through the point of fixation in the caricature. The two arcs crossing the parabola are interrupted at the horizontal axis. The upper two arcs are parabolic and represent quasi-circles in the lower quadrant of the field of view. The lower two arcs apply similarly to the upper field of view. Again subject to the flattening procedure, these arcs are always concave in the direction of the point of fixation in the laboratory specimens.

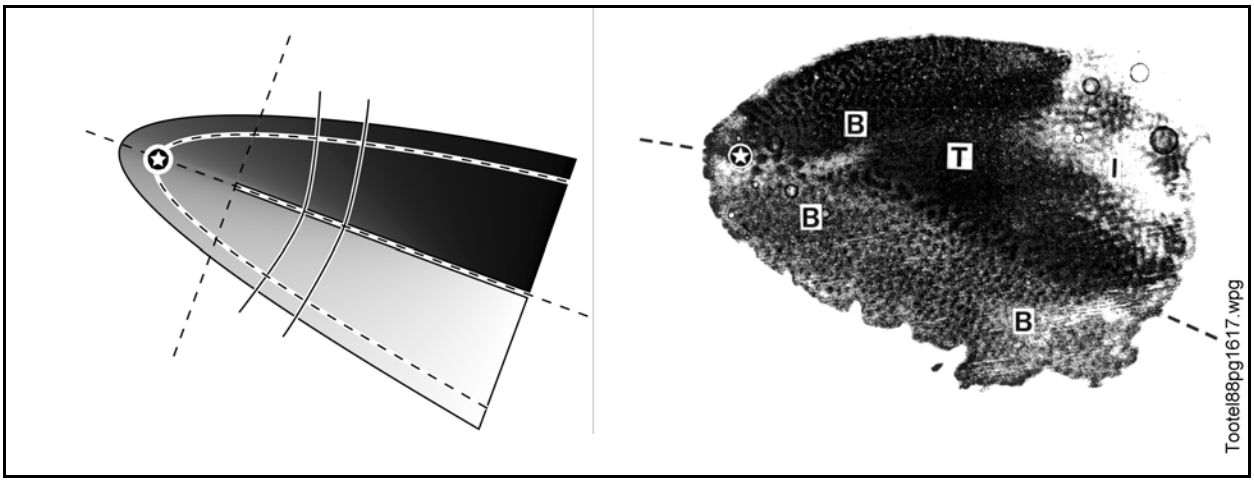

Figure 15.6.5-4 Visuotopic projection onto striate cortex showing horizontal discontinuity. Left; parabolic conformal transformation rotated 20 degrees. Parabolic curve through point of fixation (star) represents the vertical meridian. The straight dashed line pointing toward the point of fixation represents the horizontal meridian. Right; Figure 4 (pg 1617) of Tootell, et. al. 1988, showing DG uptake in operculum. Upper half was exposed to a 4.4 cycles/degree moving grating in the inferior quadrant of object space. Lower half was exposed to a 0.9 cycles/degree moving grating in the superior quadrant of object space. See Tootell, et. al. for other notation.

Figure 15.6.5-5 shows the data of Dow, et. al. at an expanded scale in the area of the point of fixation (coordinates HM:VM::0:0 describe the point of fixation). The parabolic form of the vertical meridian, bisected by the horizontal meridian, is in good agreement with the proposed parabolic conformal transformation.

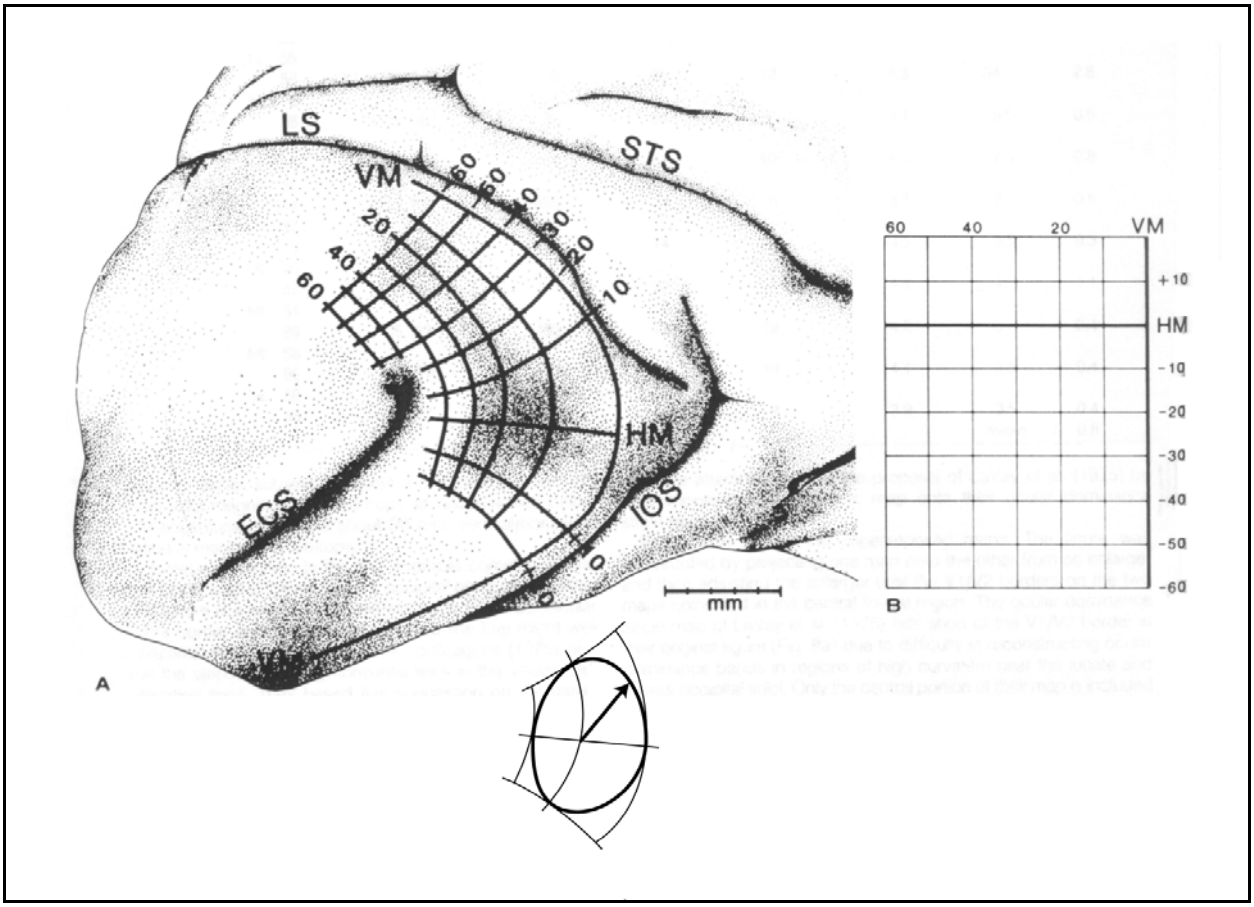

Figure 15.6.5-5 Visuotopic projection near point of fixation on one operculum of striate cortex of rhesus monkey. Numerics are in minutes of arc from the point of fixation. Grid lines were superimposed upon an artist's tracing of the right occipital operculum. ECS, external calcarine sulcus; IOS, inferior occipital sulcus; LS, lunate sulcus; STS, superior temporal sulcus; HM, horizontal meridian; VM, vertical meridian. B, The region of object space mapped onto the brain surface in A. From Dow, et al., xxx.

Because of the limited resolving power of the DG technique, Tootell, et. al. speculated on whether the point of fixation was located along the vertical meridian in their tests and also whether the point of fixation was at the edge of the operculum. If it were not at the very edge, and coincident with the point of fixation associated with the other operculum, there would be two distinct representations of the point of fixation within the one striate cortex. The figure from Dow, et. al. shows clearly that the point of fixation is not at the extreme edge of the operculum. This supports the position that there is a small amount of overlap between the two projections. Such an overlap is compatible with the medical problem of some individuals. These individuals observe a shimmering edge in the area of the overlap when a failure to merge the data from the two eyes at higher cognitive centers occurs. This duplication along the vertical meridian is discussed more fully in **Section 15.2.5** of "Processes in Biological Vision." See also **Section 18.8.2** in "Processes in Biological Vision" with regard to aura.

The data of Dow, et. al. clearly show the nature of the CMF in *Macaque* as a function of position within one degree of the fixation point. The CMF is described by the largest elliptical shape that can be drawn around a given intersection in the above figure that is tangent to the adjacent coordinate lines. The CMF in a given direction is given by the radius of the ellipse in that direction. The CMF along the HM is clearly different from that along the VM. The vertical magnification was 1.37 times the horizontal magnification at that point. For a fixed density of neurons in the underlying striate, this fact would suggest that the *Macaque* has a slightly higher spatial resolution

capability in the vertical direction. While they noted the magnification became more isotropic, and lower, away from the point of fixation, there was a distinct change in CMF with position in the field. The magnification was consistently higher near both extensions of the vertical meridian. Their measurements did not extend far enough from the point of fixation to determine whether there was any asymmetry in the CMF between the superior and inferior fields. However, the data of Tootell, et. al. and the nature of a rotated parabolic (or logarithmic) conformal transform would support such an asymmetry. The data of Tootell, et. al. and of Dow, et. al. do not appear adequate to determine whether the parabolic or the logarithmic transform better model the visual process.

Dow, et. al. presented a discussion of the relationship of various signal processing engines to locations within the striate cortex. However, the analyses provided by Schwartz are more significant. He shows that the unique properties of the conformal transforms lead to a conceptual solution to the scaling, translation, projection and orientation problems. Each of these properties is represented by a relatively straight line on the striate projection. As a result, most of these properties can be sensed by a row of cells summing into one cell. The output of each of these summing cells describes a distinct feature of the image projected onto the striate cortex. As Schwartz summarizes, "The cortical map is not 'distorted,' but is mapped by the geometry of the complex [conformal transformation], both locally and globally.' In this regard, he stresses the functional architecture of the projection process. It aligns the image with the rows of neurons comprising the striate cortex. In this role, Schwartz defines the morphology associated with the projection process as computational anatomy. In this context, the bundles in the optic nerve, the chiasms of the optic nerve and Meyer's Loops are examples of computational anatomy.

Figure 15.6.5-6 shows the effect of using the logarithmic transformation on the geometry of images presented to the cortex. In the first example, the two squares are significantly larger than the fixation point. As a result, they are imaged onto both halves of the striate cortex as shown. Note the primary difference in their images is one of position, not size or shape. Note the same condition for the second example, rotation. The difference in their position is primarily one of position, not orientation. The same situation applies to the properties related to projection and translation. These various properties all become simpler properties related to the position or orientation of a line. The striated structure of this portion of the cortex is particularly well adopted to analyzing lines. The striation is believed to be due to the predominance of long neurite and axon structures lying parallel to each other and interwoven with other neurites and axons at various angles.

Schwartz also estimates the number of individual columnar units on the surface of the striate cortex. In this work, these would be described as individual engines. They each contain 10,000 to one million neurons in multiple layers.

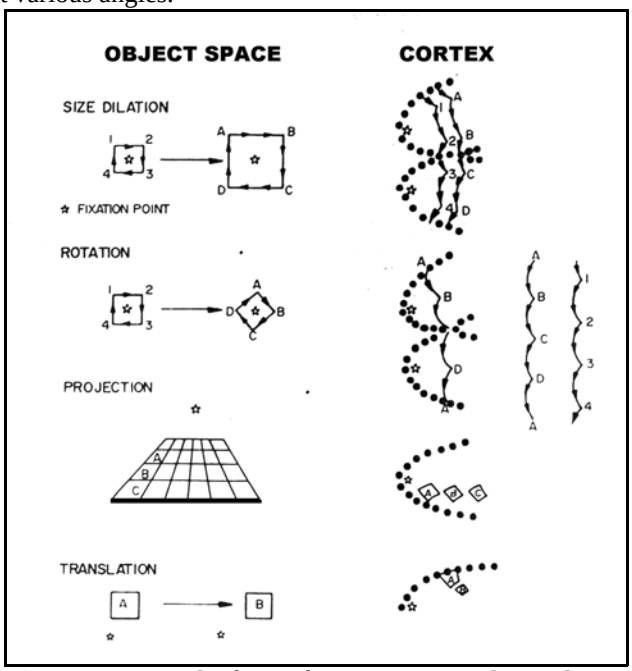

Figure 15.6.5-6 The form of images projected onto the prestriate area of the *neo*-cortex using the logarithmic transformation. See text. From Schwartz, 1980.

15.6.5.3.6 Wide field topological mapping

Schwartz reviews the mathematical language associated with conformal mapping but takes a narrow view. This view is not in consonance with geodetic map makers. The problem is with the word conformal. The mathematician frequently limits the term to local conditions in order to insure there are no discontinuities in the area. The map maker uses the term to insure the overall map is representative of the original topography. Schwartz maintains that a mapping is conformal if it is locally isotropic. If locally isotropic, infinitesimal angles are preserved everywhere in the mapping. However, a truly conformal mapping is isotropic at any scale and both large and small angles are preserved. The difference is critically important in mapping where the error in conformality is an important parameter.

Schwartz relies upon the Riemann mapping theorem based on an interesting assumption. He says "since it states that given any two planar brain regions (e.g., retina and cortex) there is a unique conformal mapping between them which is specified by the shape of the regions. . . ." It is important to note that neither the retina or the cortex are planar. On the other hand, the word planar appears unnecessary. The Riemann mapping theorem is not limited to planar surfaces. It is also important to note that this theorem is stating that there is a unique

mathematical relationship between two arbitrarily shaped surfaces. It is not stating that they look alike or are in any way conformal from the perspective of a map maker.

Schwartz recognized the "compression" of the peripheral portion of the visuotopic projection onto the striate cortex. However, he did not relate it to any model of the visual system. He introduced a conceptual correction factor based on his original logarithmic transformation. The resulting equation can be labeled a bi-logarithmic transformation in the nomenclature of Kober, e.g., the ratio of two logarithmic expressions of the form (log (θ + a))/(log (θ + b). Schwartz notes that his application of the logarithmic transforms "are based on 'isotropy': the local cortical magnification must be a scalar, i.e., independent of local direction." However, the data of Dow shows this is not the case for the monkey. There is a significant difference in magnification factor with direction at the point of fixation.

An alternate explanation for the observed compression is based on the application of Snell's Law to the transform of object space into retinal space. There is no requirement for isotropy in this formulation. In this case, the retinal eccentricity, θ, relative to the point of fixation, can be written as θ = arcsin (sin ψ)/1.33 where ψ is the eccentricity in object space. This transform can be incorporated into the simple logarithmic transform of Schwartz or the parabolic transform introduce in this work. The form of the two corrections is quite different. This is illustrated in **Figure 15.6.5-7** where the computed normalized cortical magnification factors are shown.

The conceptual logarithmic compression factor, using b = 50 degrees as suggested by Schwartz, is seen to fall off quite rapidly for small angles of eccentricity and then decreases more slowly. The Snell's Law based compression factor maintains a more nearly constant amplitude initially and then falls off more rapidly. The choice between these two corrections should be obvious when compared to the empirical data.

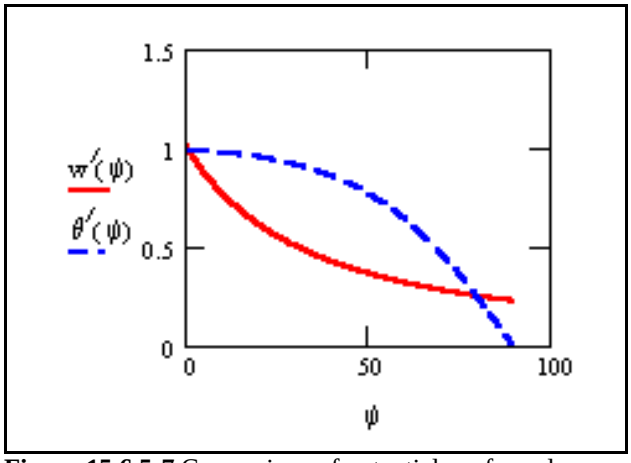

Figure 15.6.5-7 Comparison of potential conformal transform compression factors. The functions shown correspond to the local magnification factors in the images at the eccentricities, ψ. w(ψ) shows the compression introduced by the bi-logarithmic transform suggested by Schwartz. θ(ψ) shows the more significant compression introduced by Snell's Law.

Schwartz has reviewed the values of the variable "a" in his bi-logarithmic transformation appropriate to a wide range of empirical data. He notes there is little consistency between the values best fitting the different data sets. He notes differences of "1000%." The problem seems to be as much with the conceptual basis for the parameter as it is with the data. This work proposes the concept of the fovea and foveola are foreign to the imagery of the striate cortex. The imagery associated with the foveola is processed in the PGN/pulvinar couple and not in the striate/$V_{>2}$ couple.

15.6.5.3.7 Features and mechanisms within the striate cortex

With the above background, the extensive material of Tootell, et. al. presented in 1988 provides additional perspective. They begin by defining a number of terms related to the neural organization within the striate cortex (pg 1532). Their definition of a "hypercolumn" remains somewhat abstract. However, their definition of a blob is useful. "A cytochrome oxidase (cytox) 'blob'" (also known as a puff, a patch, or a spot) is an anatomical entity found prominently in the upper striate layers." They define "one cytochrome oxidase blob plus half the surrounding interblob area as a 'blob domain'." They conclude, "the hypercolumns are probably related more closely to the dimensions of a blob domain than to measurements of physiological spread."

Their inference that a "'duplicated' vertical meridian would mean that areas of the visual field near the vertical meridian are represented twice in striate cortex, . ." is of little significance except following trauma. The left and right fields of view are merged in the abstract domain. This interpretation of the process avoids their discussion of a 2:1 model versus a 1:1 model to account for the apparent over-representation of the foveola in the striate cortex. Normally there is no difficulty as a result of this merging. This merging in the abstract domain is compatible with the words of Tootell, et. al., "Simpler possibilities are that. . . the anatomical projections to the 'wrong' hemisphere are functionally suppressed. . . ." In the case of trauma, the duplication may aid in the preservation of vision along the vertical meridian.

Tootell, et. al. noted that "about 40% of our animals have no significant lateral calcerine fissure, . ." This

emphasizes the fact that fissures and sulci may cause inconvenience to researches but the underlying neural processes and mechanisms ignore them.

Tootell, et. al. note that the uptake of DG is coincident with the edges of their finite width imaged patterns, supporting the fact that the visual system is a change detector, not an imager. The extrapolation of their measurements of CMF conform to those of Dow, supporting an asymmetrical CMF at the point of fixation. Their figure 10 (pg 1544) suggests the ratio between the CMF's along the vertical and horizontal meridians remains 1.37:1 out to at least five degrees.

Care should be exercised in interpreting their autoradiographs of patterns recorded when the eyes were intentionally divergent (pg 1548). It could be assumed that the resulting image on the striate is used to correct for stereopsis. This work proposes that this error is normally removed using signals from the LGN. They also note that the fidelity of their autoradiographs is on the order of 100 microns (FWHM). This value is considerably larger than the size of the individual neurons of the striate cortex. Their discussion of the resolution capability of the Macaque eye were focussed on 3° eccentricity where such a large spatial dispersion would be compatible with the spatial dispersion due to other effects in the visual system. This avoided addressing the question of the considerably higher resolution (smaller spatial dispersion) found on axis. As they note, it lets them ignore the questions related to acuity and hyperacuity associated with the point of fixation. An average receptive field size of 20 minutes of arc is far below the pixel size of one photoreceptor in the foveola of the retina. It is even larger when compared to the equivalent size (the hyperacuity size) associated with the edge response of a photoreceptor acting as a change detector.

In discussing spatial frequency response to both luminance and chrominance signals, they return to the on-axis condition. Their figure 12 (pg 1584) shows excellent agreement between the psychophysically measured spatial frequency response and that measured at the striate cortex. The data shows the rapid falloff in the luminance sensitivity at spatial frequencies below one cycle/degree typical of a change detector.

They also confirm the luminance nature of the magnocellular channel signals are preserved in layers 4B and 4Ca of the striate cortex. Similarly, they showed layer 3 to be especially sensitive to chrominance changes. They did encounter one significant problem in their baseline. Using changing color stimuli, they did not observe any rolloff in DG uptake with eccentricity. They said, "this lack of DG variation with eccentricity is significant because the density of the cones falls off rapidly away from the fovea (pg 1592)." Their data does not support their assumption that color sensitive but morphologically defined cones exist!

There are more difficult problems associated with their color studies (pgs 1569-1593 and 1594-1609). First, they used a tricolor monitor (Tektronix 690) to generate their imagery. This monitor only uses three discreet phosphors. Thus, to obtain a particular color, say CIE equivalent values x= 0.318, y=0.586, there is no actual spectral color present at this wavelength. A mixture of two broad spectral colors are mixed to achieve the equivalent value as read on a specific spectrophotometer. Second, the coordinates they used for green, CIE 0.318, 0.586 is far from saturated green, no matter whose definition is used. Both their yellow and green values would significantly excite both the M- and L-channels of biological vision. As a result, the Q– chrominance channel, a differencing channel, would receive little excitation. In their experiments comparing the uptake to a equiluminant gray, the uptake due to such a yellow or green stimulus would not excite the chrominance channels significantly but would excite the luminance channel. Thus, they would cause an uptake virtually identical to the equiluminant gray signal. This was their strongest (and most unexpected) of the DG effects discovered in this study (pg 1591)." Here again, their assumption appears to be that the visual system employs additive signal processing based on the CIE model. Their conclusions on page 1591 based on this assumption are not supported here. However, their last paragraph, based on an alternate "color-opponent process," is supported here, used in the above commentary and satisfies their test observations.

In Part IV of their paper, they speak of a low (<10%) contrast achromatic signal was used to stimulate the retina. It must be noted that a three-phosphor monitor relies upon the psychophysics of the human visual system to simulate specific colors. It is impossible to generate an achromatic stimulus using a tri-color monitor! It is only possible to generate a signal *that matches an achromatic signal at a given color temperature when viewed by an appropriately adapted visual system.* As a result, their findings are a bit less definitive than they might have hoped for. In particular, their discussion of relative contrasts probably requires a recapitulation based on their use of a tri-color monitor and their apparent lack of control of the state of chramatic adaptation of the subjects.

Their caricatures in figures 9 & 10 (pp 1606-07) are quite useful and reproduced here (in modified form) as **Figure 15.6.5-8**. The modifications are to add the excitation of layers 5 & 6, which they defined in the text but not the caricature, and arrows indicating the flow from the occipital lobe back to the LGN. The fate of signals generated in layers 5 & 6 are of great interest in this work. They note that the signals from layers 5 & 6 generally

project subcortically. The large number of these signals passing from the occipital lobe back to the LGN are defined in more recent research (see **Section 15.6.1**). They provide the basis for the concept of the LGN/occipital lobe couple of this work. In this concept, the signals projected from layers 5 & 6 constitute abstract signals extracted by the striate cortex. Other signals returned to the old brain from MT, V2 & V3 (see below) would constitute additional abstract signals. While the diagram indicates distinct luminance and chrominance inputs to the striate cortex, the signal paths returning to the diencephalon may carry abstract signals that combine both luminance, chrominance (and quite probably orientation and scale) information.

Their captions for these figures read “Information from the magnocellular LGN layers projects into 4Ca, and from there it projects into all portions of 4B and weakly into the blobs of layers 2 and 3, and into blob-aligned portions of 4A. Information also projects strongly into layer 6.” “Information from the parvocellular LGN layers projects into striate layers 4Cb and 4A, largely or entirely bypassing layer 4B, projecting richly into all portions of layers 2 and 3. Parvocellular information also projects strongly into layers 5 and 6.” More specifically, they note that magnocellular activity spreads uniformly throughout layers 4B, 4Ca and 6 in a fashion that is relatively uniform. Magnocellular activity projects weakly into the blobs of layers 2 and 3, but not into the interblob regions of these layers. Layers 4B and 6 project to area MT, and layers 2 and 3 project to V2.

They note that signals represented in area MT are almost uniformly direction-selective and color-insensitive. They also note signals represented in area V2 are quite different; they are often color-selective, infrequently direction-selective, and sometimes disparity-selective. These descriptions are suggestive of the more abstract nature of these representations. There is no suggestion that these areas are visuotopic, only that they are responsive to features. The signals from these areas are returned to the old brain as abstract vectors that can be included in a more global saliency map.

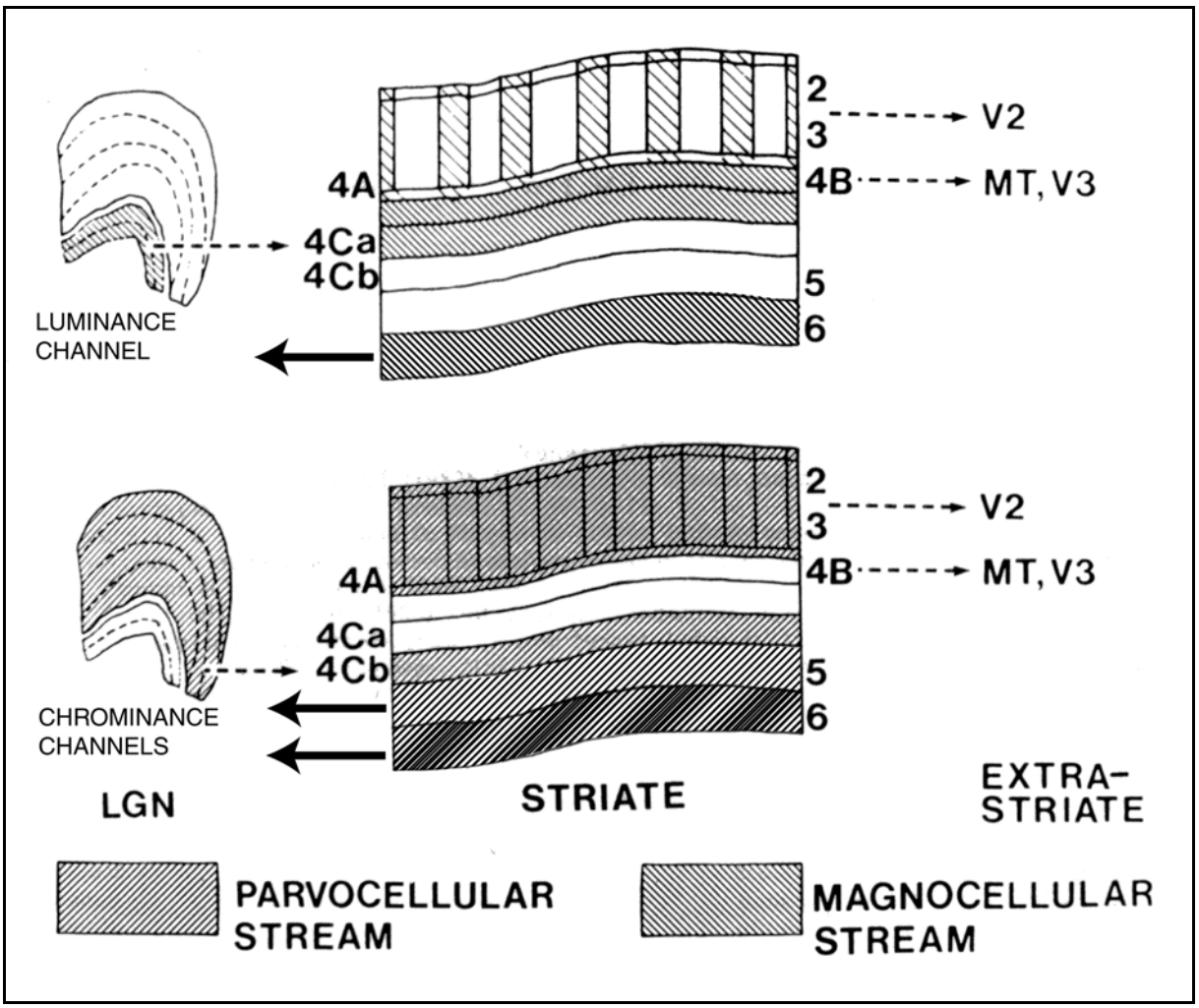

Figure 15.6.5-8 Signal flow between the LGN, striate cortex & V2, MT & V3 based on DG evidence. See text. Modified from Tootell, et. al., 1988.

In discussing the DG technique, they note it has at least two advantages over the use of horseradish peroxidase, HRP, as a tracer. The DG results span synapses that block the flow of HRP and are therefore transneural. Thus a more global representation of neural connections can be obtained. Second, the DG technique labels all of the neurons of the visual system involved in one experiment at one time. This greatly simplifies the investigative process and the time to obtain results.

Part V of their paper focuses on the parameter of spatial frequency and the striate cortex. The term spatial frequency is used more in concept than in fact. There is a subtle difference between the expression spatial frequency and spatial pattern; both of which are used in their abstract. The neural system is not capable of transcendental calculations. No investigator has ever shown how a spatial frequency can be computed from the spatial patterns presented to the visual system. On the other hand, complex summations of spatially related signals at specific times in the temporal dimension are quite easily performed. Thus, convolutions are easy, Fourier transforms are apparently impossible.

> It should also be recalled that gratings are a laboratory convenience but virtually never found in nature. It has only been during the last one percent of man's existence that groups of equally spaced parallel lines have appeared in his environment. It is highly unlikely that the basic visual system was designed to accommodate such a visually unusual pattern.

It is proposed that when Tootell, et. al. speak of high spatial frequencies, they are actually referring to closely

spaced spatial patterns. Similarly, low frequencies refer to more widely spaced patterns. Even more specifically, they are usually referring to the edges associated with these patterns. This subject is addressed specifically (pg 1610) when they note that physiological and psychophysical evidence does not support the encoding of images by (global) Fourier analysis. They note that recent work has concentrated on the scope of the receptive fields of cells. The profile of such fields need not be monotonic in spatial dimension. Recent research has identified cells that have up to 10 (spatially) alternating excitatory and inhibitory subregions. The term spatial tuning is actually a description of the character of the convolution properties of the receptive field of a cell. The term "spatial pitch selectivity" would be more useful. Such cells can produce an abstract output signal that describes the periodicity of a pattern. Based on the rotated logarithmic or parabolic conformal transform discussed above, the cells could also produce an abstract signal describing both the location, periodicity and orientation of the pattern. If correct as described, this capability provides a powerful mechanism for describing the texture inside a contour extracted by a separate feature extraction engine. As a result, the method of "painting" a complex line drawing is beginning to emerge.

They have found that cells tuned to fine spatial patterns (high spatial frequencies) are located predominantly in transmembrane columns located within the interblob regions. They suggest, based on logic, that cells sensitive to coarse spatial patterns (low spatial frequencies) would be located within the blobs. They showed that the sites within the blobs were cylindrical, those outside were more annular. It would be good to determine, through a third test, if the diameter of the annulus was proportional to pattern fineness (spatial frequency).

They did reconfirm a difference in relative size of the inferior and superior fields of the striate projection. However, there was no indication of how the CMF changed with position. They did quantify a difference in DG uptake with field position when using gratings as test targets.

They provide a thorough discussion of the uptake of DG in the layers of the striate cortex but did not provide a caricature. It is important to recall the source of their stimuli. Use of a tri-color monitor as a source can lead to poor delineation between luminance and chrominance signals as defined in this work. They found that the periodicity of the patterns influenced what part of layer 4C was most affected. Short periodicities (high frequencies) caused more DG uptake in layer 4Cb than in 4Ca. Long periodicities (low frequencies) produced DG uptake that was much higher in 4Ca than in 4Cb.

Their conclusions related to the spatial selectivity of the individual engines of the striate cortex remain preliminary but very informative for subsequent researchers.

A highlight of their discussion is the description of a "transition zone" in the region of 3° eccentricity. A transition zone, of some sort, in this region is frequently described in the medical literature.

Based on Tootell, et. al. and Schwartz, it is clear that the striate cortex is a major feature extraction engine that generates a large number of abstract output signals describing the scene presented in object space. The parabolic or logarithmic conformal transformation is a key element in the process of feature extraction.

Crawford has also presented data based on the DG technique[134]. However, it is much less comprehensive that the Tootell, et. al. papers. While it presents a more detailed structure of the deoxyglucose molecule, its caricature of the occipital lobe of monkey is not compatible with the more detailed maps of Tootell, et. al. or the parabolic conformal transform of this work. Crawford does not address the location of the vertical meridian in his discussion. However, he does suggest the locations of the two points of fixation are at the lateral extremes of the striate cortex. As a result, the visuotopic projection beyond about 10° from the fixation point are found within the calcarine sulcus of monkey. A similar arrangement for the human is confirmed by Nolte & Angevine (pg 124, fg 1). However, their caption appears to mislead concerning the location of the point of fixation. This point is established more clearly in a recent Tootell & Hadjikhani paper[135]. Unfortunately, their figures show flattening of the brain by slicing the occipital lobe along the horizontal meridian of the striate cortex. This distorts the shape of V1 significantly. A more representative figure would be obtained by cutting along the V1/V2 juncture in the style of Maunsell & Newsome[136]. Their representation clearly separates the striate cortex, V1, from the remainder of the occipital lobe. Crawford makes the assumption that the DG enters individual

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[134]Crawford, M. (1985) Sitmulus-specific columns in monkey visual cortex as revealed by the [^{14}C]-2-deoxyglucose method. Chapter 8 *in* Peters, A. & Jones, E. *Eds*. Cerebral Cortex. NY: Plenum Press

[135]Tootell, R. & Hadjikhani, N. (2001) Where is 'Dorsal V4' in human visual cortex? *Cerebral cortex*, vol. 11, pp 298-311

[136]Maunsell, J. & Newsome, W. (1987) Visual processing in monkey extrastriate cortex *Ann. Rev. Neurosci*. vol. 10, ppp 363-401

neurons and provides the necessary energy via internal processes. Crawford does extend the discussion of blobs and other transmembrane columns into area 18 of the occipital lobe.

The work of Tootell, et. al., Schwartz and Crawford all converge on a basic feature extraction engine size of about 0.5 mm diameter and the thickness of the membrane of about the same value. This calculates out to about 3000 of these basic engines in the striate cortex of monkey. For an effective neuron diameter of 10 microns, this would correspond to about 125,000 neural circuits per engine. At this size, the entire striate cortex would contain about 400 million individual neural circuits.

15.6.5.4 The SC/cerebellum *couple* of the mesencephalon EMPTY

The superior colliculus has primary responsibility for converting instructions received from the higher cognitive centers and other elements of the midbrain (under TRN supervision) into commands understandable to the rest of the efferent nervous system. The instructions from higher cognitive centers typically originate in the FEF of the prefrontal cortex, are passed to the premotor cortex, and are then passed to the primary motor cortex[137]. The primary skeletal motor cortex appears to be located in Brodmann's area 4. The primary oculomotor cortex is generally associated with Brodmann's area 7.
Robinson presents detailed maps related to the direction of subsequent saccades following stimulation[138]. He also XXX

Wirtschafter & Weingarden have provided some detailed profile maps of the human visual system[139]. By probing the cerebellum, they have located elements of certain reflex actions. Excitation of lobule V causes upward saccades and excitation of lobule VI & VII causes downward saccades.

15.6.5.5 The MGN/temporal lobe *couple* EMPTY

15.6.5.6 The Precision Optical System loop EMPTY

[xxx refer to Chapter 7]

15.6.5.2.3 MOVE The control point (aka TRN for sensory, Hypothalamus for other autonomous)

Comparing the above figure to those in **Section 7.3** and to [**Figure 15.6.5-2** below], the importance of the control point as an element in the Precision Optical System becomes obvious. It is difficult to find figures highlighting the key location of these elements morphologically.

Whenever a situation is encountered that the pulvinar cannot provide an appropriate interp, or the cerebellum cannot provide an appropriate set of skeletomotor instructions, it is desirable for the POS (including the two-dimensional correlator) to examine the object in detail under a different set of conditions. Such an examination may even call for a change in the position of the head or body to achieve a different visual perspective. These decisions are all made under the control and "veto power" of the control point.

15.6.6 The operational roles of the TRN, and the PGN/pulvinar & SC/cerebellum *couples* in vision

[xxx part may belong in 15.4]
This work introduces a functional role for the old brain that has not been presented before. The material in this section is therefore largely a proposal. Previously, many investigators have associated a variety of correlating and analytical functions with either the retina or the neo-cortex. In some work, the broader label cortex was used without further delineation. It is proposed that these papers can frequently be reinterpreted in terms of the

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[137]Fuster, J. (1993) The Prefrontal Cortex, 3rd ed. NY: Lippincott-Raven. pg 220
[138]Robinson, D. (1972) Eye movements evoked by collicular stimulation in the alert monkey. Vision Res. vol. 12, pp 1795-1808
[139]Johnston, C. & Pirozzolo, F. (1988) Neuropsychology of eye movements. Hillsdale, NJ: Lawrence Erlbaum Associates pp 5-15

important roles played by the PGN/pulvinar couple (pretectum) and the SC/cerebellum couple in vision, and using the block diagrams of this work. In this work, the PGN/pulvinar couple plays a crucial role in the higher visual capabilities of man, other higher primates and possibly other higher chordates. It is the mechanism that extracts the interps, the most basic intellectual information about an image presented to the foveola of the retina. The interp goes beyond the simple information extraction capability shown by some animals based on coarse shape and color information. [xxx Similarly, the cerebellum plays a crucial role in the ability of the human, and other higher chordates, to relate these interps to their historical experience. In the case of the cerebellum, these interps are not limited to vision. Areas of the cerebellum have been isolated that relate to all of the senses. However, the relationship is one of response to a command, not one of feature extraction from afferent signals.

The highest chordates employ a level of capability and cooperation between the PGN and the pulvinar that is not shared with any other animals. The level might be considered symbiotic. While the PGN is capable of extracting interps associated with specific symbols imaged on the foveola, it does not appear to contain the memory necessary to relate these interps to its previous operation. The pulvinar appears to be the main memory associated with the conversion of the geometrical parameters related to an interp into a percept. Whether it does this on a individual interp basis or is able to associated interps in order to achieve a more comprehensive percept is yet to be determined. It is not clear yet whether the pulvinar contains sufficient memory to relate sequences of interps into a single percept. However, the subdivision of the pulvinar into a series of subunits suggests it is able to process both individual "basic" interps and higher level interps.

Because of the limited knowledge in this area, the PGN/pulvinar couple can only be considered as classical "black boxes" at this time. Initial efforts can be made to define the signals going into and coming out of each box. It may also be possible to bound some of the processes occurring within each box based on our knowledge of some of the performance parameters achieved by the "boxes." These will be the primary goals of this section.

Figure 15.6.6-1 shows two potential signaling paths attributable to the foveola/PGN/pulvinar pathway. It is possible that some signals related to stereopsis (**Section 7.4.5**) may be extracted from the left and right PGN prior to precision information extraction relating to the scene centered on the point of regard. However, because of the complexity of the information within the field of the foveola centered on the point of regard, it would be expected that the data would be merged prior to information extraction within the pulvinar (as in the upper frame).

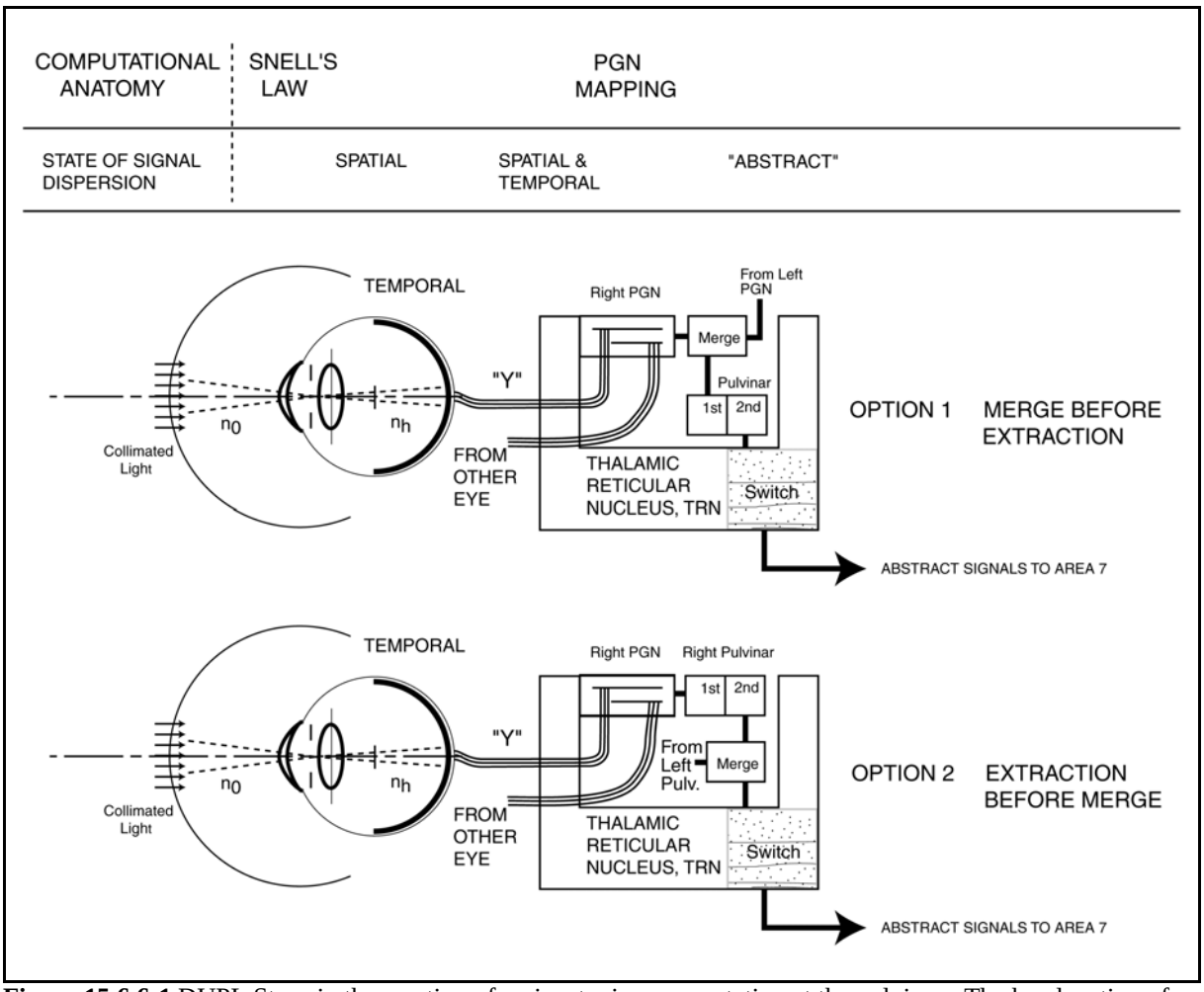

Figure 15.6.6-1 DUPL Steps in the creation of a visuotopic representation at the pulvinar. The key location of the TRN is shown. The label "Y" is used to indicate the propagation of all of the UV–, S–, M – & L– channel signals from the foveola directly to the PGN. The upper frame suggests merging of the signals from the right and left PGN before forwarding to the pulvinar for precise information extraction. The lower frame suggests precise information extraction within each pulvinar before merging the data and passing it to the pulvinar. See text.

Section 19.10.5 of this work discusses the recent academic investigations attempting to model the information extraction activities of the neural system within the context of a large scale digital computer. The purpose has been to improve current methods of extracting information from two (or three) dimensional imagery for purposes of machine reading and information extraction. Most of the circuitry employed in those studies is totally foreign to the actual non-transcendental circuitry of the neural system.

15.6.6.1 Overview of the perception mechanisms related to the foveola of vision

Figure 15.6.6-2 provides additional conceptual detail relative to the analysis tasks of vision. The major feature of the figure is its separation of the analysis tasks related to bucolic scenes from those related to the unique skills of humans to recognize abstract symbols regardless of scale and particularly near the limit of visual acuity. This latter capability is further dissected to reflect the specialized training required to accomplish these specialized tasks.

As noted by Robinson & Cowie, "The vast majority of the neurons within the pulvinar subdivisions respond to visual stimuli. However, many of these same cells receive other inputs which modulate their visual excitability. The functional contributions of these modulations can be viewed as contributing to the generation of signals

about salience." This view is supported totally. It is proposed that the ancillary inputs are from other sensory sources and the resultant vector contains information from both visual and other sources. The pulvinar provides the first "machine language" representation of what is "seen" (or more broadly--perceived) by the subject, the initial interp.

From a different perspective, Robinson & Cowie also propose that most of the responses of the pulvinar neurons are generally binocular although the proportion of binocularity differs among primate and carnivore species. This is probably because of the higher degree of common visual field in primates than other mammals (including many carnivores).

Their further discussion, with respect to attentional factors, is difficult to interpret without knowing much more about the particular experiments. They may be reflecting a change from the semi-automatic analytical mode of "routine" vision to a more volition driven analytical mode. Their discussion on pages 67-86, which includes the terms overt and covert attention, suggests this is the case. They also discuss some of the first uses of PET scan techniques to evaluate the performance of the pulvinar.

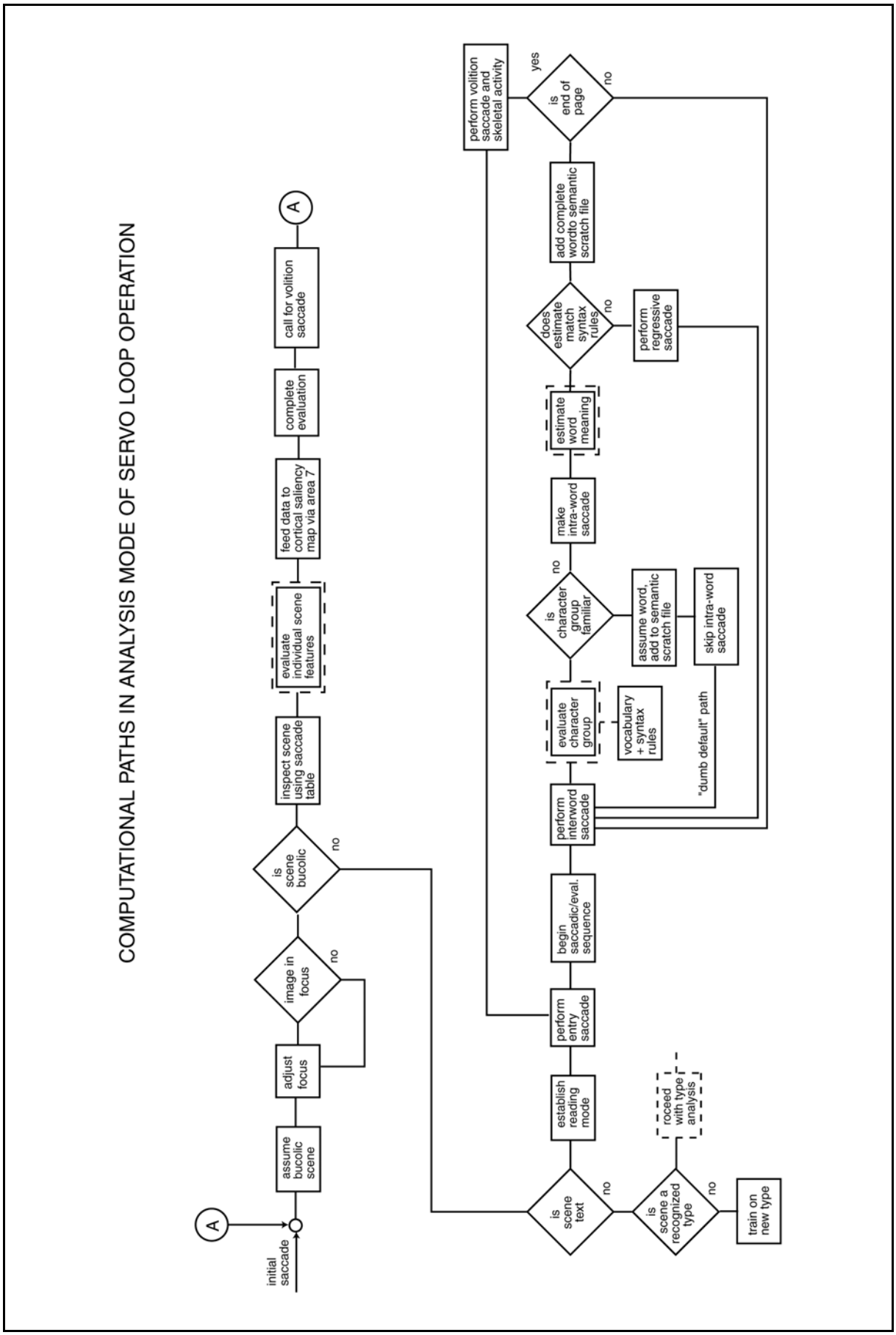

Figure 15.6.6-2 Computational paths and engines associated with perception. Note the double box around those elements of the system responsible for the actual perception of objects and symbols.

They conclude with a brief discussion, with references, of the considerable visual capability of even tree shrews and hedgehogs following removal of the striate cortex. This compliments earlier discussions in this work of the presence of a functional tecto-pulvinar pathway to area 7. This path is totally independent of the striate cortex, is not retinotopic and involves "machine language signals. They also discuss the relationship between the superior colliculus and the pulvinar based on several conflicting investigations. They conclude with an interesting list of open questions.

The above discussion raises the question of where the precision merging of the images from the two foveola occurs in order to provide a precision vergence signal to the oculomotor system and where the results of this merging are first utilized. It could be assumed that the merging process is achieved in the TRN (or the PGN portion of the TRN) in a manner analogous to that performed in the LGN for the peripheral field of view. If true, a totally merged signal would be available within multi-dimensional correlator of the TRN/PGN for immediate conversion into an interp. This initial interp would be passed to the pulvinar, acting as a PROM. This methodology would suggest that, while the pulvinar is frequently shown as a bilateral nucleus, it may not be one. Alternately, its bilateral aspect may be due to a desire to implement a redundant capability. Logic would suggest the pulvinar is not bilateral overall but may exhibit an internal bilateral form for purposes of redundancy. Robinson & Cowie (page 63) discuss the existence of a medial pulvinar as well. Their interpretation would be compatible with this discussion.

The observation of Robinson & Petersen that 30% of the neurons of the pulvinar are excited by visual stimuli is completely compatible with the role of the pulvinar as a PROM type lookup table converting the output of the multidimensional correlator into higher level machine language. It is typical of such a device to exhibit participation by most of the cells in an overall conversion. It is only the few output signals (resulting from the underlying Boolean computations) that are significant. These output signals are only found on a handful of neurons connected to the output commissure. Robinson & Cowie address other evidence supporting this role for the pulvinar[140].

15.2.3.4xxx The "interps" and "percepts" used to facilitate cognition MOVE

Section 7.5.5 [xxx check this citation] has discussed the role of the PGN/pulvinar couple and POS in the process of analyzing images presented to the foveola of the eye. The discussion focuses on mechanisms not previously discussed in the literature. Because of this, it is necessary to define new terms suitable for that discussion. **Section 15.4.1** of this chapter will use those terms to develop the subject further. Those terms also apply here. The output of the PGN will be described in terms of "interps." An interp is a vector signal generated by the PGN as a result of a cross correlation of the information provided to it from the foveola. An interp results from the correlation performed during a single gaze interval, measured in milliseconds. These interps are accumulated in a short term memory associated with the saliency map. This memory is used to assemble interps sequentially until a "percept" is formed. A percept is the vector message passed to area 7 of the cerebral cortex for purposes of recognition and further cognition.

King has provided data suggesting the merging of the initial percepts from the visual and aural system, into at least a portion of the saliency map associated with current events, occurs in the midbrain[141]. He describes the melding of signals between various sensory systems in the superior colliculus. This would appear logical since it would aid in the generation of oculomotor system drive signals based on alarm channel signals from **all** sensory systems. These responses would not be encumbered by the time delays associated with signals traveling to higher cognitive centers and back. It would also aid in the storage of important percepts in the pulvianr for recall at appropriate future times for purposes of threat and pattern correlation.

Until further analyses are performed, it will be assumed that a portion of the saliency map may reside in the midbrain. This assumption would not prevent a copy of this map being forwarded along the Pulvinar Pathway to Area 7 of the cerebrum to support the construction of a more comprehensive saliency map. The division of labor between interps and percepts will be discussed in more detail in **Section 15.6.5**.

15.6.6.2 The multi-dimensional correlator of the Precision Optical System

Earlier studies summarized in this work lead to a variety of parameters related to the multi-dimensional correlator of the visual process. This correlator is a major functional portion of the structure generally defined in

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[140]Robinson, D. & Cowie, R. (1997) Op. Cit. pgs 63 & 68

[141]King, A. (2002) Neural plasticity: How the eye tells the brain about sound location. *Current Biol*. vol.12, pp R393-R395

morphology as the pretectum *in many animals*, or the portion of the tectum receiving signals directly from the portion of the optic nerve related to the foveola *in all chordate animals*. This correlator is called the perigeniculate nucleus, PGN, in this work. There may not be signals related to a foveola in some of the lower chordates.

It is proposed that this correlator receives signals related to approximately 23,000 photoreceptors found in the central portion of the fovea. This central portion of the fovea, the foveola, involves a nominal diameter of 1.18 degrees centered on the line of fixation of the eye. The photoreceptors in this area transmit their signals directly to the correlator over a sequestered part of the optic nerve. They may also provide signals to other luminance and chrominance channels proceeding to the LGN. However, the primary role of these photoreceptors is to support the analytical function of vision performed in the PGN and tied closely to the pulvinar.

The signals received by the PGN from the Stage 3 projection circuits of the optic nerve are sequential, and temporally band limited, in character. Each signal is recovered from a sampled data mechanism. Each signal is spatially independent of each other. While the signals contain no absolute lightness or brightness information because of the zero in the transfer characteristic of the adaptation amplifiers, the signals contain both temporal, spatial and brightness information about the scene encoded in a very complex arrangement (see frequency foldback in **Addendum–Interferometry**). It is assumed that the frequency of the action potential stream, the emblem of the instantaneous brightness driven temporal sampling process, from each photoreceptor is independent

No spatial correlation related to the analysis mode is performed in the retina with respect to the above signals. On the other hand, the spatial information from the retina has been encoded in these signals by the motion of tremor. The spatial position of the individual photoreceptors in the foveola and the single tremor motion used to encode the signals at all photoreceptors insures that the individual temporal signals contain a degree of signal correlation. It is this correlation that allows the correlator to extract the information related to the image presented to the foveola. The characteristics of the Stage 3 projection circuits play a role in limiting the performance of the correlator. These limitations may be beneficial in preventing, or eliminating some ambiguities in such a sampled data system. A prime goal would be elimination of Moire effects due to either the temporal sampling and/or spatial sampling mechanisms.

It is proposed that the correlator delivers two types of output signals, as mentioned earlier. Its primary role is in extracting interps from the full set of signals delivered from the foveola. It has a secondary role in extracting high quality stereopsis related signals to complement the role of the LGN in this area. It also has the task of extracting signals defining the distance to the scene element of maximum interest and providing these signals to the accommodation function within the POS. In some cases, the correlator may be tasked with providing the signals required to repoint the eyes in order to bring a secondary scene element (within the 1.18 degree diameter viewed by the correlator) to the center of the field of view of the correlator.

[xxx rewrite after changind drawing]
Figure 15.6.6-3 provides an initial description of the multi-dimensional correlator of the PGN. The input is shown as a bundle of ~ 23,000 individual circuits from the input commissure (the optic nerve). The primary output will be considered a bundle of individual circuits (of unknown order) providing signals to a node between the processing engines of the diencephalon, the cerebellum and the neo-cortex. This node is labeled the control point in the figure. Its complexity is much larger than indicated. This control point is the command center for the entire nervous system. Its function is frequently associated with the morphologically defined hypothalamus. The secondary outputs are bundles supporting the accommodation and vergence functions of the oculomotor nuclei. They are passed to the Edinger-Westphal area via the Superior Colliculus. From there, they go directly to the individual oculomotor muscle control circuits.

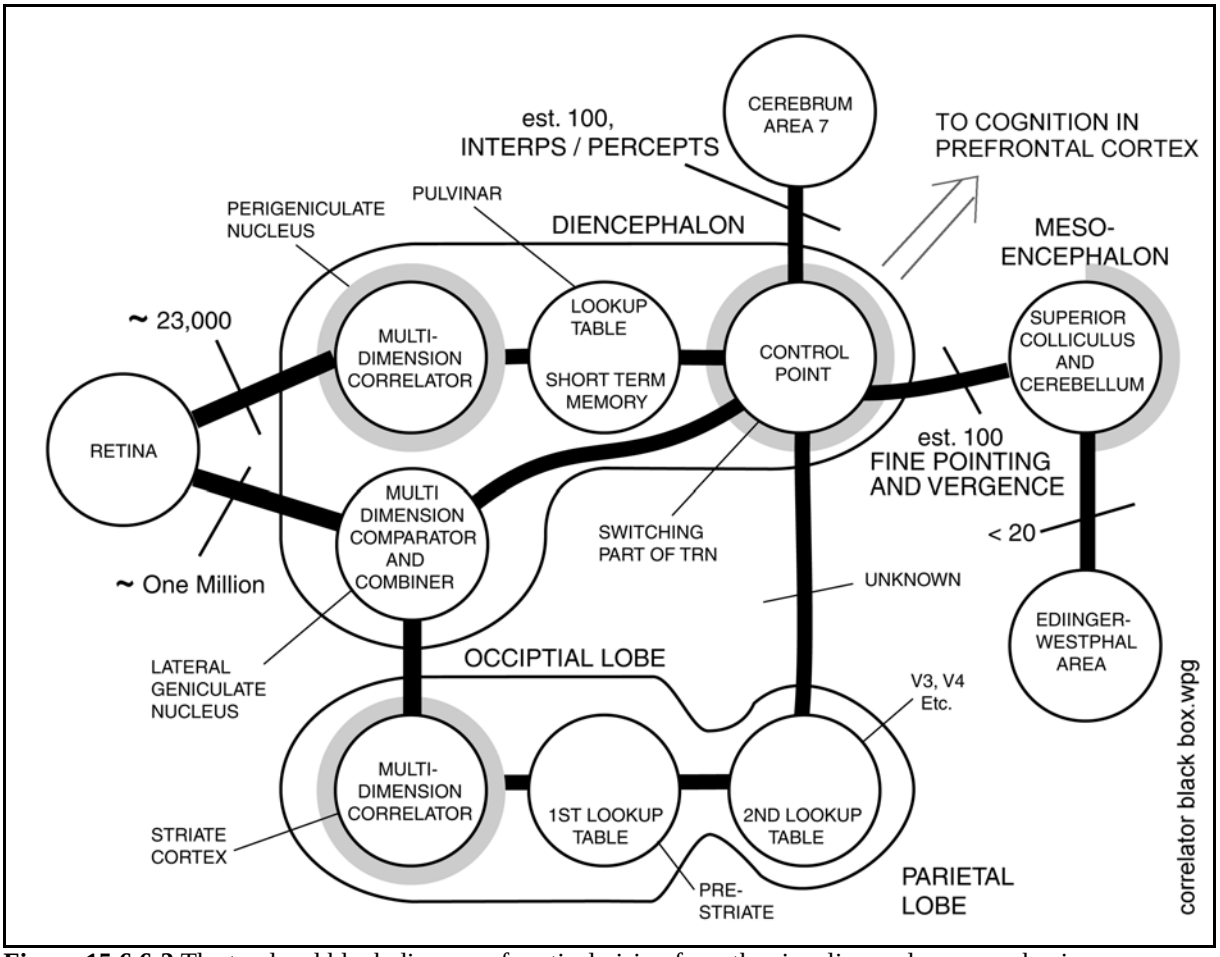

Figure 15.6.6-3 The top level block diagram of cortical vision from the signaling and servomechanism perspective. The functional descriptions of the individual boxes remain as in Section 15.6.1. The number of individual neurons in each commissure are only estimates of various degrees. Based on the previous discussion, the conceptual control point is synonymous with the switching portion of the morphologically named thalamic reticular nucleus. See text.

The estimate of the number of neurons passing along the Pulvinar Pathway to area 7 of the cerebrum is based on the expectation that the number of neurons connecting the multidimensional correlator and the pulvinar is quite large. This expectation is based on the assumption that the coupling between the correlator and the memory circuits of the pulvinar is quite close and that these elements perform the majority of the computations required to arrive at a comprehensive percept(s) describing the observed scene (relative to the foveola). It is only this high-level percept that need be transmitted to the neo-cortex.

15.6.6.2.1 Potential modes of signal acquisition

The method of signal acquisition at the retina and the architectural design of the correlator found in the pretectum are closely tied. There is no current information available on the precise character of the tremor used to generate the temporal signals at the photoreceptors from the image projected on those receptors. The last comprehensive work was by Yarbus and Ditchburn in the 1960-70's. **Section 7.3.6** through **7.3.8** discuss their work and reviews the requirements related to signal acquisition for purposes of analysis mode operation.

15.6.6.2.2 Detailed parameters of the multi-dimensional correlator

[xxx re-edit next three or more para now]
The candidate architecture discussed above suggests that the pretectum contains a multi-dimensional correlator organized very much like those found in the LGN. However, it operates over much shorter time cycles (typically

50 msec for simple image material) and may be very hard to explore by probing. In common with other cortical tissue, it probably consists of about six layers. Each layer would represent a different short term memory map of the scene imaged on the foveola. These would be dynamically cross-correlated to generate a best estimate of the line structure of the image every 50-100 msec. This estimate would be output as an initial (basic) interp. It appears these interps would be addressed as a group on a 200 msec cycle time. The result would be an interp that could be transferred to the 2nd lookup table of the pulvinar for additional correlation processing leading to a percept.

The question of whether the basic interps are input into a second correlator (providing short term memory), in order to create a more comprehensive interp, is open to discussion. The location of such a second correlator is also an interesting question. Similar questions can be raised concerning the assembly of initial (basic) percepts into more complete percepts. Does this occur in the pulvinar or is this where the cerebrum comes into the picture?

The candidate architecture would suggest the multi-dimensional correlator of the pretectum would contain multiple individual planes associated with different short time intervals. These "time planes" would be processed to obtain a best estimate of the line elements of the image in real time with an output occurring at a nominal frame interval of 50-100 ms, (see discussion to follow). The approximately 23,000 photoreceptors supporting the correlator would suggest that each plane of the correlator can process a two dimensional array of binary signals with a diameter of approximately 175 elements. If each pixel element occupied 25-36 square microns, the correlator would only occupy one square mm of cortex surface. A correlator of this size would be very small relative to the size of the LGN correlators. With a time cycle of 50-100 msec and the unknown form of the analog signals employed, this correlator would be very difficult to locate by the typical probing used in conventional electrophysiology experiments. If a stabilized image is projected onto the foveola, the output of the correlator would actually go to zero because of the bandpass characteristics of the input signals. Lacking any knowledge of the code format, locating the correlator by its phasic output signals would also be extremely difficult. It is likely it will be located initially using traffic analysis of signals between it and the pulvinar (probably via the control point).

Pairs of time planes can be compared by summing along various diagonals of the overall array. No data on the lateral extent of such diagonals is available, but a figure of ±5 pixels per pair of planes can be adopted for discussion. This value would suggest the multidimensional correlator could operate at nominal levels over a pixel range of 175 - 2·n·5 without encountering edge difficulties. The factor n represents the worst case number of planes along a single diagonal. This suggests a nominal correlator with full performance over 125-150 pixels. This number can be compared with the values discussed in **Sections 7.5.3** and **17.8**. It suggests that the correlator can process a 3-5 letter syllable at high levels of accuracy within 50-100 msec during reading.

It is premature to try to describe the detailed circuits of the correlator.

15.6.6.2.3 Edge effects related to the multi-dimensional correlator

Any finite dimension correlator has problems in implementing its full capabilities when it approaches the edges of its data set in any of its dimensions. This appears to be the case in one class of amblyopes studied by Srebro (See **Section 18.1.2.1.1**). It may also suffer from limitations on the quality of the information supplied to it.

Williams has provided some interesting information with regard to the limitation of the correlation functions at maximum spatial bandwidth applied to the foveola. In discussing the visibility of interference patterns imaged on the retina, he provides a useful scenario. Parts of it are excerpted below:

> "In the range between 0 and 45 c/deg or so, the interference fringe can be seen across the entire field. . . As spatial frequency increases from about 45 c/deg, the bars of the fringe can be seen only in a progressively smaller region of the filed that moves with the eye and is centered on the line of sight.
>
> At roughly 60 c/deg, the fine, regular bars ar lost in the spatial noise that characterizes coherent fields. . . .At 60 c/deg and retinal eccentricities beyond the central 3 deg of the fovea, some observers report a faint granular appearance , resembling non-oriented, two-dimensional noise. Also, most observers report the appearance of an annulus of extremely fine wavy lines whose diameter is roughly 2.5 deg, centered on the line of sight. A drawing made by the author depicting the appearance of the annulus at 80 c/deg is shown in fig. 4(a).
>
> As spatial frequency increases, this annulus of wavy lines shrinks, finally collapsing to a

circular patch at a frequency of 90-100 deg. Observers describe this patch as resembling a fingerprint or pattern of zebra stripes. Figure 4(b) and (c) show drawings of the appearance of a 110 c/deg interference fringe made by the autor and a naive observer respectively. The scale bar in the drawing represents 1 deg visual field.

The zebra stripes maintain a fixed configuration at a given spatial frequency and drawing made of them weeks apart reveal the same pattern. . . ."

Figure 15.6.6-4 reproduces figure 4 from Williams that highlights these comments. It is modified to include the nominal diameter of the foveola of this work (1.18 degrees) and a larger circle at 2.2 degrees. These circles are nominal values irrespective of the signals applied to them.. Also added are the two pairs of boxes illustrating the phase and frequency ambiguity introduced by the sampling process inherent in the visual system The significance of these boxes will be discussed following the next section.

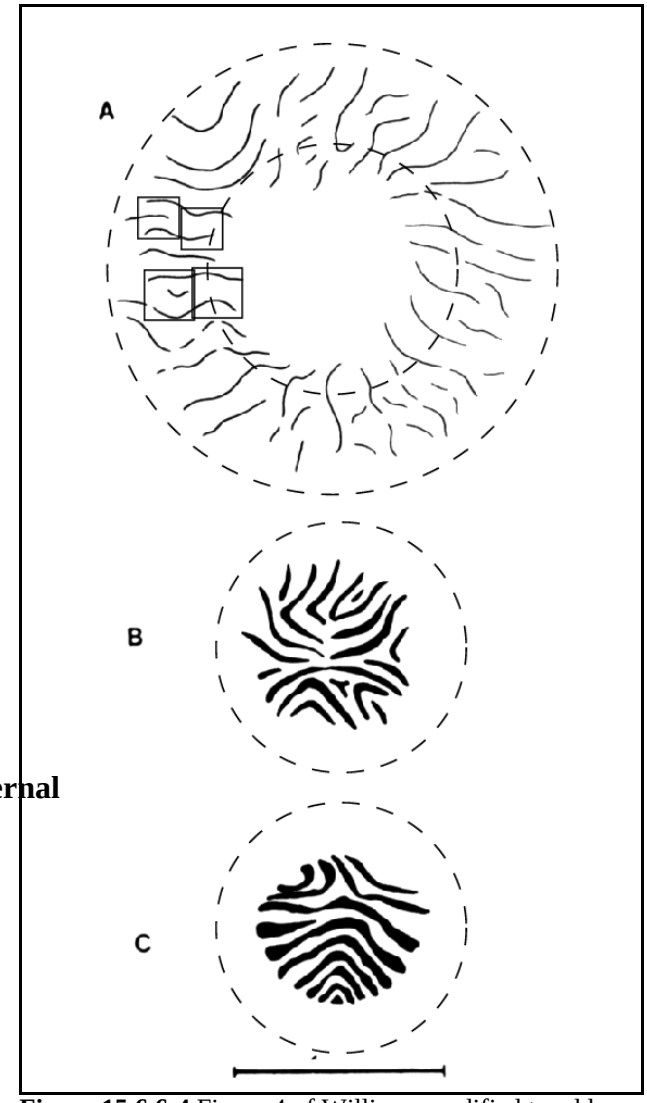

Figure 15.6.6-4 Figure 4 of Williams modified to add reference circles. (a) Williams' drawing of the appearance of an 80 c/deg interference fringe. (b) Williams' drawing of the appearance of a 110 c/deg interference fringe. (c) Drawing made by a naive observer of a 110 c/deg interference fringe. Scale at bottom correspondes to 1 deg visual angle. Smaller circle represents nominal 1.18 deg diameter of foveola, larger circle represents 2.2 deg.

15.6.6.2.4 Role of Moire Effect internal to vision

Because of its common appearance in image reconstruction, particularly commercial television, many investigators have tried to define the role of the Moire Effect in the biological vision system. The scenarios and mechanisms proposed to date to account for, or more specifically account for the absence of, the Moire Effect in vision have been less than successful. By separating the effects of sampling at the retina from the potential Moire Effect in the putative image reconstruction process, a better understanding of the potential role of the Moire Effect in vision is possible.

Reviewing the earlier discussion, the Moire Effect is an artifact of a superposition process. It can occur in any data with any number of dimensions. It is fundamentally involved in the appearance of absolute maximums and absolute minimums occurring at regular intervals as the result of summing two repetitive waveforms. In television, it is personified by diagonal lines appearing in the reconstructed imagery. In music, it is personified by the beat note observed if a musical instrument(s) is not tuned properly. While it is not necessary for the nominally spaced maximums and minimums be absolute; if they are not, their impact is quickly masked by the presence of the other asynchronous waveforms.

As discussed with regard to the neural channels supporting the analytical mode of operation, color is not considered when processing the signals in the correlator. The analytical mode is color blind. The cognition channels rely upon the achromatic signals from the analytical mode and the chromatic signals from the awareness mode to provide a complete "picture" of the imaged data.

It is proposed here that the two-dimensional correlator employed in vision does not attempt to reconstruct the image projected on the foveola of the retina (there is no little green man to look at the **re**-constructed image). Alternately, its role is to **de**-construct the previously sampled image into its critical geometric parameters.

The reason for this is the visual system is based on a change detector architecture and not on an imager architecture. As discussed in terms of the scanning, associated with tremor, used to obtain signals for the two-dimensional correlator, the system employs edges of the spatial patterns imaged on the foveola rather than maximum and minimum amplitudes in the deconstruction process. This difference can be illustrated in **Figure 15.6.6-5**.

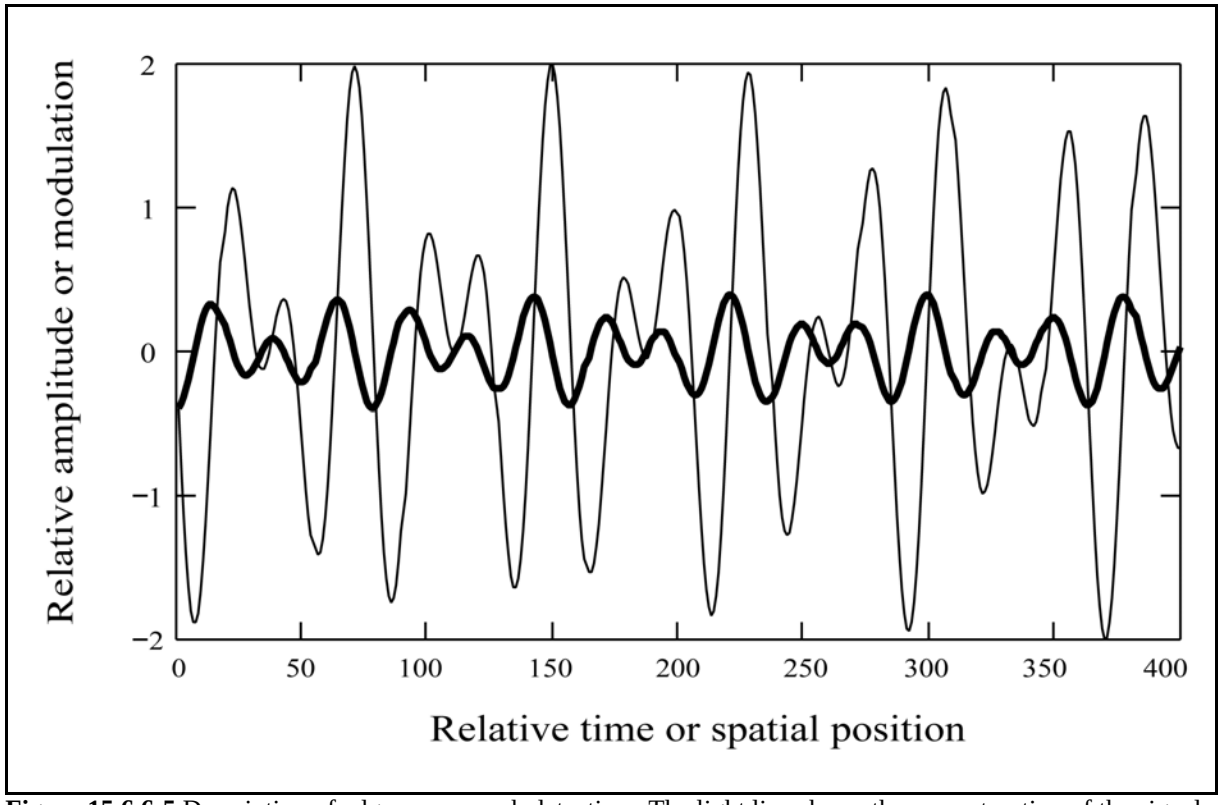

Figure 15.6.6-5 Description of edge versus peak detection. The light line shows the reconstruction of the signals from the foveola by an image re-constructor. The absolute maximums and minimums occurring every 75 units form a distinctive Moire pattern not present in the original image data. Alternately, the heavy solid line represents the output of a change detector representing the same original image data. It shows much less impact due to the Moire Effect. If this signal is processed by a zero crossing detector, no Moire Effect will appear in the output.

It appears that the correlator accepts the change detector data from the foveola and then, using a zero crossing detection circuit, precisely locates the edges in the image data. The output of the correlator is a series of lines of finite length at angles defined by the graininess of the two dimensional correlator. Samples of this result are shown in **Figure 15.6.6-6**. If a character is imaged on the foveola at limiting acuity, the correlator outputs a signal consisting of simple lines generally connected at various angles.. If the character is imaged at somewhat larger size, the dual stick character illustrates the form of the basic interp. At larger sizes, the interp may contain auxiliary information derived from the signals of the awareness channel. Each of these examples are defined as basic interps in this work. The correlator is able to process about 3-5 characters at a time. Thus, the primary output of the correlator is an interp consisting of 3-5 basic interps. This interp is then processed at a higher level (assumed here to be in the 2nd lookup table of the pulvinar, but possibly in the parietal lobe) to forms percepts that can be addressed by the cognitive centers of the anterior lobe of the cerebrum. This figure is discussed in a broader context in **Section 17.8**. The code used to output the interps and the percepts is unknown at this time.

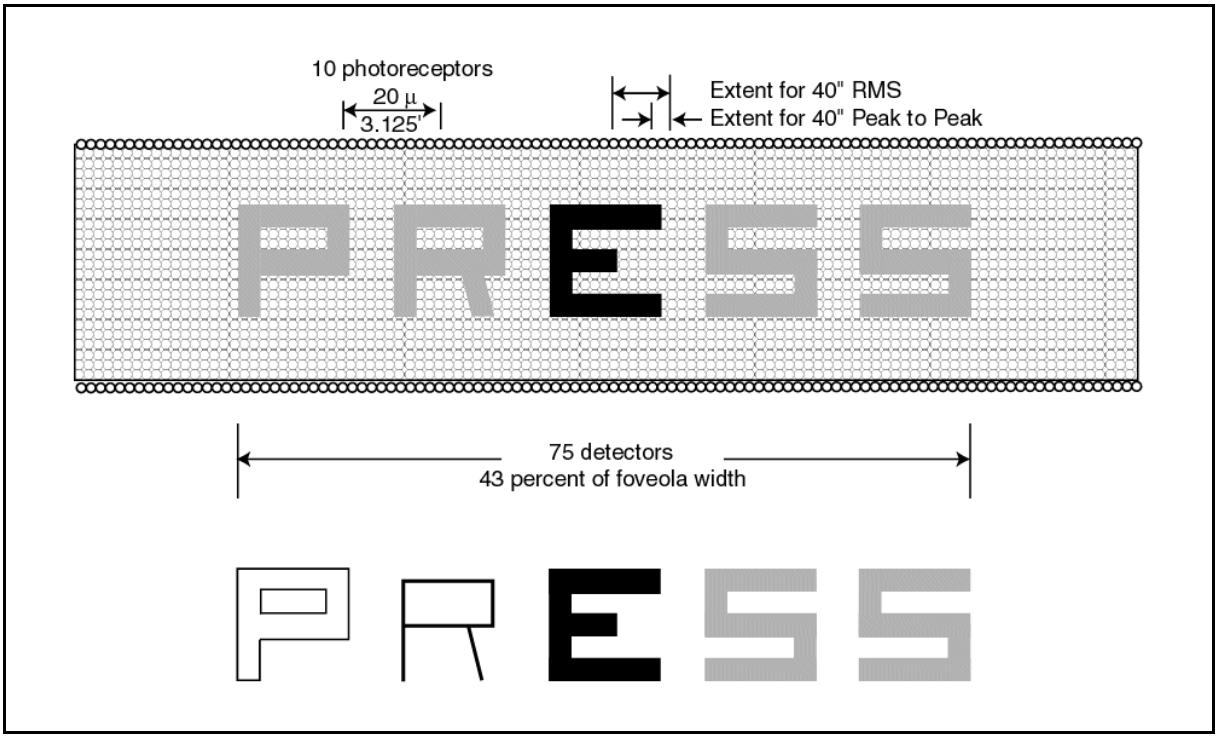

Figure 15.6.6-6 Representation of the image projected onto the foveola as a function of size. Lower row shows the stick variant reported at limiting acuity, the double stick variant reported at image sizes greater than limiting acuity and the filled characters reported for even larger sizes in cooperation with the chromatic information from the awareness channel.

In conclusion, it is useful to state several proposals. A clear distinction should be made between the Moire Effect related to superposition of two patterns and the phase error effect associated with inadequate sampling of finite duration waveforms. It is proposed that the Moire Effect plays no role internal to the biological vision system. Because the pretectum operates as an image de-constructor instead of an image re-assembler, the output of the correlator and the pulvinar do not exhibit any Moire Effect.

15.6.6.2.5 Discussion of the interferometer results of Williams

Before reviewing this section, the reader must be familiar with the Fourier Transform and its various attributes, especially those associated with the two-dimensional plot of spatial frequency frequently found in the literature.

Williams has relied upon a foundation provided by a simple algebraic analysis in Snyder and Snyder & Miller that is addressed in detail in the above section. The interpretation of the above papers should be reviewed before proceeding. **Section 16.6.3** provides a substantive review of this area.

With the above concepts in mind, along with the fact that the data from the foveola and the peripheral retina are merging in a region surrounding the foveola (see **Section 2.6.1**), the data of Williams can be analyzed. Looking first at (a), the field drawn extends form about 1.0 degrees to about 2.2 degrees. The test set was adjusted to illuminate a 2.0 degree field on the retina. Williams did not specify explicitly the orientation of the fringe pattern in these figures. However, the horizontal lines at the two sides would suggest the fringe extended vertically. The lines are drawn as thin lines. This would suggest several points. First, this is an area (normally extending to a larger outside diameter) known to involve the merging of data processed separately by the foveola and the ex-foveola. A degree of confusion would not be unexpected in this area.

Section 18.8.6.4 discusses the clinical condition that appears related to this psychophysical phenomenon. **Sections 2.6.1 & 18.8.1.2** relates this condition to the phenomenon known as macular sparing.

Second, the pitch between the lines are representative of the actual pitch of the fringe pattern. The fringe pattern frequency was set to 80 cycles/degree. The frequency of the fringe pattern is above the Nyquist (ambiguity limit) but below the Nyquist frequency limit for the vertical axis of the array. Third, there are probably phase errors indicative of non-uniformities in the array factors of the retina in this area. The errors in this frame are primarily phase errors due to the quality of the close-packed hexagonal array of the retina. This suggests that the Nyquist frequency of this retina, along a vertical axis, is above 80 cycles/degree.

Looking now at (b), the situation is different in several ways. First, the lines are much higher in contrast and the pitch between lines is less, even though the fringe frequency was raised significantly to 110 cycles/degree. The pitch and the broadness of the lines suggests they are formed by frequency-fold-back. This suggests that the Nyquist frequency of this retina is below 110 cycles/degree. Since the pitch is less than that in the left and right portions of frame (a), it is reasonable to determine the fold-back-frequency is above 80 cycles/degree. There is significant phase error suggesting there are irregularities in the orderliness of the photoreceptor array of the foveola similar to those in the surrounding area. These pieces of data suggest the vertical Nyquist frequency of the eye of D.R.W is between 95 and 100 cycles/degree (See the following comments regarding Yellott before accepting this empirical estimate). This value is consistent with the other comments in the paper related to D.R.W observing spatial frequencies up to 200 cycles/degree, the amplitude ambiguity point associated with the second harmonic of the Nyquist frequency. It also appears consistent with the contrast sensitivity function shown in his figure 3. Frequencies in the range of 100 to 200 cycles/degree would involve frequency-fold-back but still be readily observable at an apparently lower frequency. Based on the Nyquist frequency of 95-100 cycles/degree, the Nyquist (ambiguity) limit would be near 50 cycles/degree (based on the Yellott measurements, it would be closer to 55 cycles/degree).

Using the above numbers, the center-to-center photoreceptor spacing, for D.R.W can be calculated if the focal length of his eye were known. Using the Blaker focal length (for a gradient index based system) of 17.78 mm as an expedient, and the formula for the Nyquist frequency (not the Nyquist limit) related to the minimum dimension axis of a close packed hexagonal array,

$$\text{Nyquist frequency, } \nu_N = 2/(s \bullet 3^{0.5})$$

The calculated center-to-center spacing is 1.79 microns for ν_N = 100 cycles/degree. If the LeGrand focal length, for an unaccommodated eye and a uniform gradient lens is used, the spacing would be 1.68 microns.

> The above equation is usually not defined precisely (especially when compared to the Nyquist limit defined above) and gets kicked around quite a bit in the literature. Williams uses the equation with one in the numerator to calculate the Nyquist Limit. Hirsch & Curcio (1989) use four to calculate the Nyquist frequency.

Under the alternate assumption that the in-line axis of the close packed hexagonal array is the appropriate axis used in this experiment, the square root of three would be replaced by two. The calculated center-to-center spacing using the Blaker focal length would then be 1.55 microns for ν_N = 100 cycles/degree.

These are measured, in-vivo, values based on psychophysical experiments involving the entire visual system. The primary error concerns the true focal length for D.R.W. compared to the nominal values used.

It is not clear why Williams used a photoreceptor diameter of three microns to calculate his Nyquist limit of 56 cycles/degree in his paper. While this is a typical number for a peripheral outer segment, Polyak shows clearly that the outer segments of the foveola are less than one micron in diameter and on the order of 1.5 microns in

center-to-center spacing[142].

Yellott has provided a direct method of determining the Nyquist frequency of the eye (see **Section 16.6.3.5**). His experiments relied upon micrographs of a human retina *in-vitro* and without a record of the orientation of the retina *in-vivo*. His results show clearly that the human eye exhibits different Nyquist frequencies along different axes of the eye. The locus of the Nyquist frequency was at 110 cycles/degree (presumably along the three major axes of the close spaced hexagonal array) and at 128 cycles/degree along an axis defined by Snyder & Miller. Using the Yellott technique and the *in-vivo* photomicrographs such as those found in Roorda & Williams[143], it is possible to unambiguously measure the Nyquist frequency of any eye along each of its principle axes (relative to the mosaic) and with respect to the horizontal and vertical meridians of the eye.

The phase errors in frame (b) of the above figure are difficult to interpret without a similar drawing representing data obtained with an orthogonal fringe pattern. If the above patterns were the result of a sampling array formed by two orthogonal axes, the interpretation could be easily extended based on this additional data. However, the close packed hexagonal form of the retina contains three non-orthogonal axes. The precise mathematical description of the errors in the array would probably require fringe patterns spaced at 120 degrees in angle. The lower part of frame (c) is particularly suggestive of a 120 degree symmetry.

Lacking the additional data, it is interesting to superimpose a square mask designed to include about three dark lines of each of his patterns. This has been done for two adjacent areas in frame (a) of the Williams figure. Note the left box of each pair shows three bars within the boundary, and the right box shows only two (suggesting an entirely different frequency for the original fringe pattern). This is a clear example of the phase and frequency error reported in the reconstructed scene in response to a simple fringe pattern of constant line spacing across its entire width. Many other similar pairs could be highlighted in this figure. The size of the masks used may give some indication of the size of the correlation box used within the 2-dimensional correlator of the visual process.

Frame (c) is consistent with frame (b) and suggests that the parameters of the eye of the naive observer, both in dioptric performance and physical dimensions, were similar to those of D.R.W.

The discussion related to subject W.M. (Page 199) and the data in figure 3 are interesting. The subject is about 4D myopic. A correction was provided for this condition and an adjustment was made in data reduction process. However, there was no indication that an adjustment was made to compensate for the magnification change associated with this condition. W. M. exhibits a somewhat lower Nyquist frequency and Nyquist limit. The change is probably do to the physiological optics of his eye rather than a change in the spacing of his photoreceptors. However, an extended axial diameter could introduce a stretching of the center-to-center spacing of his photoreceptors. No discussion of his potential astigmatism could be found in the paper. Based on the data, it is reasonable to assume his Nyquist frequency, relative to the vertical axis, was near 80 cycles/degree and the null associated with the second harmonic was near 160 cycles/degree. Test points obtained above 80 cycles/degree would be suggestive of frequency-fold-back.

A change of 20% between the Nyquist frequency of D.R.W and W.M., due to differences in the physiological optics of the two individuals would not be outside of the normal clinical range.

It can be concluded that the broad zebra stripes in the figure are associated with frequency-fold-back caused by the application of interference fringes to the retina that were at a frequency above the Nyquist frequency of the photoreceptor array with respect to the appropriate major axis of the array. The bending in both the directly observed lines and in the zebra stripes are reflective of positional variations (phase errors) in the orderliness of the photoreceptor arrays. A more precise interpretation would require additional drawings reflecting illumination by fringes with different orientations.

The wandering of the zebra stripes are indicative of positional errors in the mosaic of the observers retina. Such errors can cause inappropriate drawing of fine detail in microscopy. Good photo-interpreters and microscopists learn that they cannot always depend on their visual system to interpret the finest details in their complex samples. They learn to draw what they see and then reorient the specimen and draw it again.

Although not discussed here, the drop in contrast sensitivity below 10 cycles/degree in figure 3 is due to the low frequency performance (in the temporal frequency domain) of the adaptation amplifiers used in stage 2 of the visual process (see **Section 17.6.3**). This performance is inherent in the neurological mechanism of the

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[142]Polyak, S. (1957) The vertebrate visual system. Chicago, Il: Univ. Chicago Press, pp 266-271

[143]Roorda, A. & Williams, D. (1999) The arrangement of the three cone classes in the living human eye. *Nature*, vol. 397, pp 520-522

photoreceptor cells and will always appear in psychophysically derived MTF's.

15.6.6.3 The SC/Cerebellum in relation to the Precision Optical System EMPTY

Hubel has pointed out that the cerebellum does not reflect the contralateral organization shared by most of the brain[144]. The right half of the cerebellum relate to the right half of the skeletal system. It is assumed that his comments apply to the visual part of the CNS as well.

15.6.7 Signal latencies among the major engines of the visual modality

[xxx Section 15.6.7 of the Neuron & Neural System has been expanded considerably over this version]
Bullier has provided a summary of the selected latencies encountered in human vision[145] based on tabular data in a separate paper[146]. **Figure 15.6.7-1** shows the graph based primarily on VEP data relating to the LGN-occipital pathway. No data is provided relating to the lower latency PGN-pulvinar pathway. The large variations about the mean can be attributed to the small number of subjects but much of the variation is probably due to variations resulting from the test protocol. Bullier notes, and the P/D Equation of this work substantiates the variation in the recorded latencies with changes in stimulus intensity. The process is reviewed in **Sections 12.5** and **specifically 12.8.2.** The equations are presented in **Section 7.2.4** where the delay can be equated to the latency of the photoreceptors alone. [**Figure 7.4.2-4** documents the sensitivity of the latency to the light level used to stimulate the outer segments of the retinas. The light level is spectrally dependent. The ambient temperature also plays a role in the latency of the photoreceptors in exothermic animals. Mathematically, the latency begins when the amplitude departs from the quiescent baseline. The theoretical and measured latencies at the output of the stage 1 sensory neurons fall in the 40ms to 70 ms range under xxx conditions. There is a unique illumination condition defined as the Hodgkin Solution which always results in an initial latency of 65 ms.

The data of Bullier clearly represents *relative latencies* since they do not include the intrinsic latency of the photoreceptors of stage 1 sensory neurons or the subsequent delays associated with stage 2 and stage 3 neurons prior to the occipital lobe and V1.

> There is a significant problem related to the Bullier figure. It directs the reader to citation #4 to support all of the data in the figure. However, this citation contains a variety of typographical or stenographic problems. The book containing the source data never appeared under the title indicated and is not listed in the publisher's catalog. Unless the references can be recovered, the paper is of very limited scientific value.

Bullier notes the early appearance of visual signals at the MT, the MST and the FEF that appear to be unrealistic if they are in fact receiving signals primarily from the "dorsal path" associated with the occipital lobe and V1. Bullier also notes, "As shown in Fig 1B, it is clear that there are a number of cortical areas, such as MT, MST, FEF (frontal eye field) and 7a that contain neurons that are activated sufficiently early to influence neurons in areas V1 and V2." This is strong support for the presence of, and lower latencies of, the PGN-pulvinar pathway.

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[144]Hubel, D. (1988) Op. Cit. pg 64
[145]Bullier, J. (2001) Integrated model of visual processing *Brain Res Rev* vol 36, pp 96-107
[146]Bullier, J. (2003Fahle) Cortical connections and functional interactions between visual cortical areas *In* Fahle, M. & Greenlee, M. *eds*. Neuropsychology of Vision. Oxford: Oxford Univ. Press

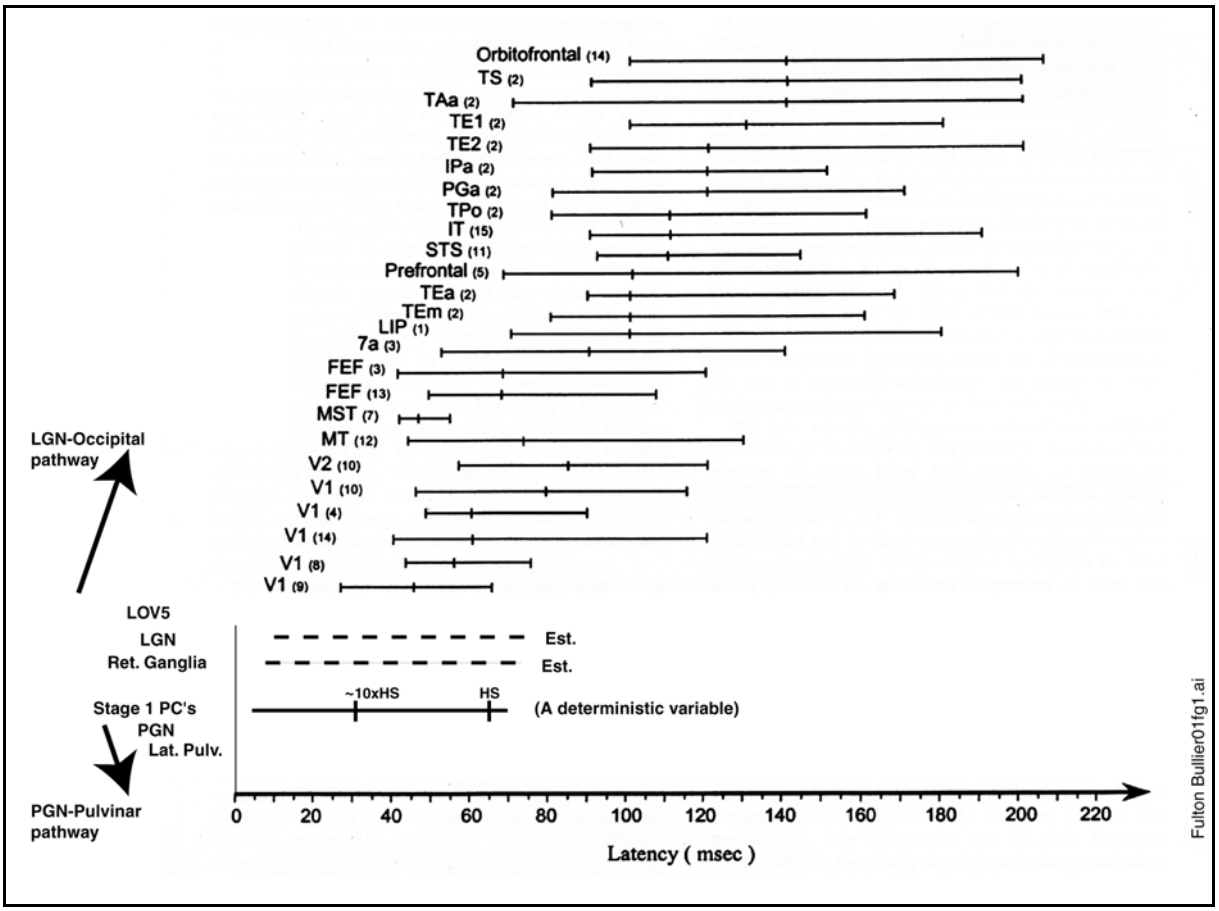

Figure 15.6.7-1 Latencies of visual responses of neurons in different cortical areas based on the LGN-occipital pathway. No data for the PGN-pulvinar pathway was included. The central tick represents the median latency with the extremes of the line indicating the10 and 90 percentiles. Numbers in parenthesis refer to bibliographic references given in Bullier, 1994. The figure has been expanded to include LOV5 defined in the Vanni et al. paper of 2004 and provide an area for the PGN-pulvinar pathway. See text. Modified from Bullier, 2001.

Vanni et al. have extended the Bullier study to include additional fMRI data from seven humans[147]. They note in their abstract, "We measured the timing of activity in distinct functional areas of the human visual cortex after onset of a visual pattern. This is not possible with visual evoked potentials (VEPs) or magnetic fields alone, and direct combination of functional magnetic resonance imaging (fMRI) with electromagnetic data has turned out to be difficult." They employed a 1.5 T MR scanner from Philips, Inc. This machine provides low temporal resolution but sufficient spatial information to optimally place VEP sensing coils. They summarize their work, "Our approach shows that it is feasible to directly seed information from fMRI to electromagnetic source models and to identify the components and dynamics of VEPs in different retinotopic areas of a human individual." Their VEP readings were at the usual microvolt levels. They noted, "Variance due to noise in the VEP signal was explained by one or two noise vectors, found at the presignal period, between 100 to + 50 ms with respect to stimulus onset (Scherg and von Cramon, 1984; Tesche et al., 1995; Uusitalo and Ilmoniemi, 1997). Careful selection of the individual noise vectors was important for discrimination of source activation in the multidipole models." After defining a new area that appears to be an association area, they also noted, "Other visual areas showed interactions appearing later than within LOV5: starting at 150 ms in V1, at 120 ms in V3-V3a for the left visual hemifield stimulation and at 160 ms for both visual hemifields stimulation." Said more directly, information related to the visual field was observed in LOV5 considerably before it appeared in V1!

[147]Vanni, S. Warnking, J. Dojat, M. Delon-Martin, C. Bullier,a, J. & Segebarth, C. (2004) Sequence of pattern onset responses in the human visual areas: an fMRI constrained VEP source analysis *NeuroImage* vol 21, pp 801–817

They encountered interpretation problems when comparing monkey and human data because of the difference in scale of the respective brains. Lacking an appropriate schematic, they did not properly account for the stage 3 signal projection circuits used for distances of over 2 mm. Because of this, they speculate, "Latency of neuronal activation is the sum of axonal delay and integration time of a target neuron (Nowak and Bullier, 1997). In monkeys, areas V1 and V2 show about 10-ms latency difference (Nowak et al., 1995; Raiguel et al., 1989), with around 4 m/s conduction latencies for feedforward axons (Girard et al., 2001). Thus, the 20- to 25-ms interval in Subject 1 cannot only be accounted for by the larger human brain and longer conduction times, but also by differences in integration time." They do provide computer unfolded representations of the brains of their subjects (1 through 7) to illustrate their findings (with the 2-cm scale bar clearly shown) in **Figure 15.6.7-2** . Any neural path approaching 2 cm must employ stage 3 signal projection technology, which includes multiple NoR action potential regenerator circuits, to avoid signal distortion or loss, and to conserve power.

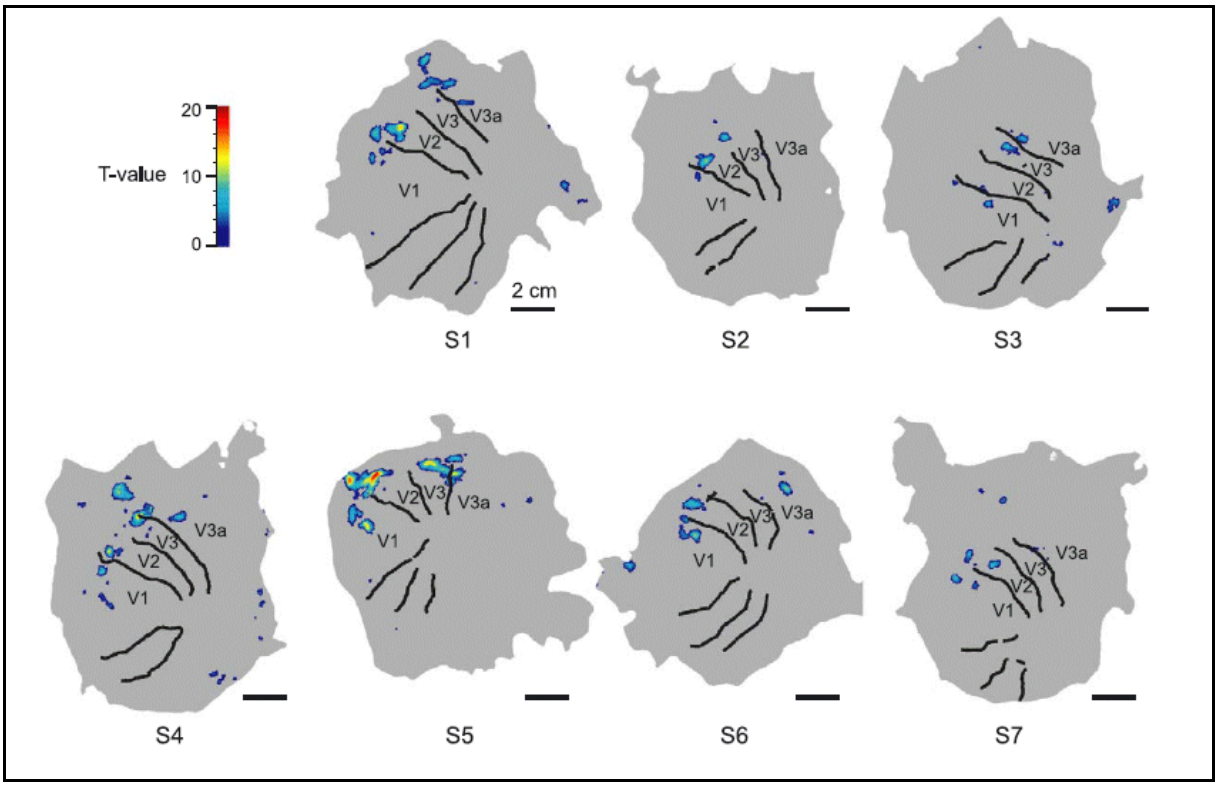

Figure 15.6.7-2 Unfolded right occipital lobes with borders of retinotopic areas and fMRI activations for D pattern displayed for all subjects. Clusters in the dorsal (named) retinotopic areas were included for seeding. Individual 2-cm bars are shown below each unfolded cortex. From Vanni et al., 2004.

The analyses of their data is quite extensive and draws a variety of conclusions. Their conclusions begin, "As a conclusion, our results show that during the rising phase of the V1 response, on average from 50 to 80 ms, there may be activation in other retinotopic areas, V2, V3, and V3a, contributing to the signal. However, contribution from these extrastriate areas seems to be weak before 80 ms and cannot be confirmed from our data because their activation may partially reflect crosstalk from V1. The LOV5, anterior and lateral to the retinotopic areas, starts activation from 60 to 70 ms onwards, reaching its first peak at 90–100 ms. In addition, with our paradigm and methods, we cannot rule out early activation from V6, or anterior cuneus, which is shown to overlap with the early retinotopic responses." They obviously encountered crosstalk from source contemporary with or preceding the activations within V1. These are attributed at least in part to signals related to the separate PGN-pulvinar-association pathway. There is no indication they attempted to evaluate the latencies related to the on-axis stimulation of the foveola-PGN-pulvinar pathway. The areas they analyzed represented a "left visual field" and a matched pair of visual fileds remote from the point of fixation (see their figure 1).

Vanni et al. have highlighted the presence of another visual pathway in their conclusion, "Our results show that the interaction between two spatially distinct visual patterns emerges first bilaterally within the temporooccipital cortex, in a region we have named LOV5 given its proximity to the lateral occipital and V5 complexes. In areas

V1,V2, V3, and V3a, the interactions due to the combined stimuli were considerably delayed. Finding an early interaction in LOV5 supports the validity of the early activation in this area reported in the accompanying paper (Vanni et al., 2004). If such an early response was due to cross-talk from the mapped areas V1, V2, V3, or V3a, and would thus constitute an artifact, we should see no early interaction between the responses to the two stimuli in LOV5 since they are not observed in the mapped areas (Figs. 7 and 8). The LOV5 source region was the same for the left lower visual quadrant stimuli and for the left and right lower quadrant stimuli (Vanni et al., 2004), suggesting that this area is the first in the human brain to combine spatial information globally, regardless the position of the stimulus in the visual field." They describe this area without having stimulated the foveola intentionally and have thus encountered the PGN-pulvinar pathway indirctly. They have also noted its low latency relative to the neurons in V1. See **Section xxx** for similar data from others.

15.6.7.1 Latencies in baseball and cricket EDIT

A lively discussion occurred in 2011 over the CVNET blog on the internet regarding the timing of events associated with a batter in baseball or cricket. There were many words provided but very few specifics and no diagrams. The discussion began with a discussion of a fast ball traveling about one foot in 7 msec or very near to 100 MPH (nominally 160 kilometers/hour). Such a pitch requires 600 msec to travel 85 feet from the pitchers rubber to the center of homeplate. To arrange for the bat to meet the ball in the center of the plate and travel into center field, these 600 ms must be allocated to, recognizing the release of the ball by the pitcher at the start and positioning the bat directly over the plate at 600 msec later. In between, the batter must determine the trajectory of the ball with high spatial precision, determine the balls nominal velocity, and calculate when to instruct the skeleto-muscular system to swing the bat precisely.

It is generally agreed within the ophthalmology community that the best batters have visual acuity in the 20/15 or even 20/10 range. This would clearly help in determining the trajectory of the ball precisely. No specific advantage in the neural system latencies of the best batters has been demonstrated.

Practice is known to play a major role in baseball batting, thus suggesting that a reflex action may be involved that largely bypasses the prefrontal lobe in responding to the pitch. A question even arises as to whether the frontal eye fields (FEF) are involved in such reflex activity. A case can be made that an effective batter employs a reflex response passing through the cerebellum (labeled the RC path in **Figure 4.6.3-1** of **Section 4.6.3**).

The batter focuses intently on the point where the ball is released and maintains the image of the ball within his foveola during a majority of its travel. These actions suggest the broader field of the fovea and the LGN-occipital pathway is largely ignored during batting. It is the PGN-pulvinar pathway that is significant. This pathway was not addressed in Bullier's analyses, or in that of others participating in the CVNET blog.

It was estimated in the blog that good hitters had to commit their swing when the ball was about 20 feet from the plate. This suggests that all calculations related to the CNS, except for those occurring within the ocular nucleus of the precision optical servomechanism (POS) must be completed while the ball is still 140 msec from the center of home plate. The question arises, does the batter calculate the actual trajectory or does he compare the trajectory with previously experienced trajectories, and use a set of commands stored in the lookup table of the cerebellum to command the skeleto-muscular system to hit the ball?

[xxx what is the conclusion? Consider adding PGN-pulvinar pathway values in a lower portion of the table.]

15.7. Extrapolations to the full brain

This work has not considered a comprehensive search of the brain literature. However, the analyses of the visual system suggest a variety of baseline parameters for the brain. It may also be showing new avenues for discussing the concept of consciousness. However, this subject remains so daunting that only a reference to Steriade and a one paragraph overview will be given here[148].

What has surfaced in this Chapter are several important aspects concerning the operation of the brain.

• First is the much greater dependence on memory in vision than is usually appreciated.

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[148]Steriade, M. (2001) The Intact and Sliced Brain. Cambridge, MA: The MIT Press, Chapter 5.

• Second is the clearer recognition that, even within one modality, the neural system does not rely upon one channel, or one circular route from sensor to motor response.

• Third, the visual system alone exhibits a considerable array of separate processing channels and mode of operation.

• Fourth, the brain relies upon a "control point," probably associated with the thalamic reticular nucleus of the diencephalon, to control the operation of the sensory, motor (and presumably glandular) systems of the subject.

• Fifth, the above control point appears to join with the so-called limbic system to form the seat of emotion.

• Sixth, the control of the response of the overall system (organism) through the thalamic reticular nucleus, and associated components of the limbic system, still leaves the whole subject of cognition and the subject of "self" unaddressed. Without an understanding of these elements, the subject of consciousness cannot be addressed intelligently.

15.7.1 The concept of consciousness

In the above reference, Steriade struggles with a viable current definition of consciousness. She says, ". . .brain causes consciousness. . .my opinion is that we do not know more at this time, and this is especially true when attempting to relate different types of neurons with consciousness."

After discussing the various proponents of consciousness based on either "awareness" or "images of knowing centered on self," she then shifts dimension, intentionally, to address the difference between first order consciousness and higher order consciousness. After spending about five pages in this area, she closes with "we will continue to work at the neuronal level and do what can be done, and much can be without reaching altitudes that would be dangerous for mentation, to no avail."

15.7.2 Top level organization

The brain is fundamentally a two dimensional sheet of neurons that consists of about six morphologically definable layers or laminates. This sheet has been extensively folded, especially in the higher chordates, in order to achieve a minimum total volume compatible with other operational and defensive considerations.

The brain appears to be organized as an asynchronous distributed modular system. The modules are grouped according to function. These groups can be described from a variety of perspectives. The most autonomous operations of the brain are centered on the oldest portion of the brain, the hind brain. The next higher level of operations, under at least partial cognitive control, are the responsibility of the old brain. The new brain, or neocortex, is responsible for a majority of two classes of operation. It is responsible for all cognition and for at least a majority of perception. A caveat applies to the closed loop operation of the servomechanism known as the Precision Optical System (Auxiliary Optical System). This system may involve some perceptual capability in order to more effectively perform its analyses of fine visual details.

[xxx
The neocortex is divided morphologically into four major areas. From front to back, they are the anterior lobe, the parietal lobe and the occipital lobe. These are supported by the temporal lobe(s) located along the sides of the cortex. Xxx The anterior lobe is primarily involved in cognitive functions of the highest order. To separate these functions from activities associated with the motor elements, Fuster has long used the term prefrontal to designate the location of the highest cognitive processes. While this designation has a number of semantic problems, he has addressed the alternatives[149].

The occipital lobe is concentrated more heavily on the steps in perception. It maintains two distinct operational structures. One operational structure is responsible for receiving and correlating signals from a variety of sensory systems. To do this effectively, it employs large areas which exhibit a coarse, and not necessarily contiguous, physical correlation to the sensory fields of each sensor. As the data is assimilated into a complete saliency map tailored to the animals needs (which may be an entirely virtual map), the map loses any correlation to any individual sensor or portion of its sensory field. The saliency map consists of vectors of unknown format at this time.

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[149]Fuster, J. (1997) The Prefrontal Cortex, 3rd ed. NY: Lippincott-Raven pp 1-5

[xxx
The saliency map is formed by the action of a series of feature extraction engines located at different locations on the surface of the occipital lobe. These engines create the saliency map via an organizational structure that can be well described as a star network. Each engine has the capability of being directly connected to every other engine. It is not possible to describe these engines explicitly as the nature of the fundamental features interpreted by the brain has only been discussed conceptually up until now. The number of engines and the number of interconnections are unknown at this time. The number of discrete feature engines may exceed several hundred in the human.

The saliency map is accessed by a series of feature interpretation engines located primarily in the anterior lobes of the brain. It appears these engines are also arranged functionally in a star network with a high degree of interconnection between themselves, with the (probably virtual) saliency map, and the feature extraction engines of the occipital lobe. These feature interpretation engines are the ultimate terminus of the afferent neurons of the system and the source of the efferent neurons controlling the actions or responses of the animal.

Most of the motor control elements of the brain, with the clear exception of the motor elements of the Precision Optical System, are found on the surface of the brain along the border between the anterior and occipital lobes. These areas are situated to receive signals from both lobes with minimal total time delay relative to the time of any input stimulus.

15.7.2.1 The declaratory memory system EMPTY

15.7.2.2 The limbic system EMPTY

[xxx Allgleton, (2000) The Amygdala. Oxfod: Oxford Univ Press traffic; voltages; kindling; assoicative learning; limbic system figure and list; neurochemistry
[xxx Mizumori (2008) Hippocampal Place Fields
[xxx Whalen & Phelps (xxx) The Human Amygdala. NY: Guilford Press Traffic Analysis; amygdala & memory; basal forebrain; anatomical org. of amygdala; quiet organ; behaviour studies; morphology

15.7.2.3 Size and number of discrete engines EMPTY

15.7.2.4 Types of discrete engines EMPTY

[xxx fundamentally analog

15.7.3 Operating modes

The brain operates primarily, by well over several orders of magnitude, in the analog signaling mode. Each engine operates semi-autonomously, receiving and transmitting signals to other engines via the star network of interconnections. Each engine appears to include its own cache memory. When considered in toto, these cache memories may constitute the total memory of the animal. No other area of the brain has been found dedicated exclusively to memory.

All of the processing of signals within each engine is performed by an immense number of unmyelinated neurons. Each neuron contains at least one Activa–and each synapse constitutes a separate Activa. These neurons appear to be at least partially grouped into separate layers within the brain. The fourth layer from the outer surface appears to be primarily responsible for interconnections with other engines of the brain. In some areas of the brain, the fourth layer has been subdivided into three or more sublayers. In general, layer 4C appears to be the nominal terminus of most afferent projection neurons. There is some indication that most interconnections between nearby engines originate from layer two or three and interconnections destined for more remote engines originate from layers five and six. Lund & Boothe have provided detailed morphological studies of these layers[150]. Some of there conclusions may require review based on the three terminal nature of a neuron.

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[150]Lund, J. & Boothe, R. (1985) Interlaminar connections and pyramidal neuron organisation in the visual cortex, area 17, of the macaque monkey. J. Comp. Neur. vol. 159, pp. 305-334

Actual signal processing appears to employ a large number of analog neurons operating in a high gain mode typical of correlation circuits in similar man-made equipment. Small groups of such circuits are easily interconnected to form latching circuits known as flip-flops. These circuits are representative of circuits employing *external* feedback. The feedback is local to only one or two discreet circuits. Such latches form the basis of volatile memory in analog based man-made circuits. A particularly simple form of latching memory circuit can be made from the same fundamental topology as found in the individual photoreceptor cells of the retina. However, the photoreceptor cells do not incorporate this modification and do not exhibit memory. The circuit is a differential pair with explicit capacitive feedback. Such a circuit can be used for memory of any duration. With this modification, only one neuron is required to provide a discrete memory element.

Because of the size of the elements involved, it is possible that a single synapse may constitute a complete memory unit. If the Activa of the synapse were of the proper size and is biased appropriately, such an active device could exhibit the Zener effect. Such a device can be considered a Zener diode. Such a diode exhibits a region of negative impedance and can be used as a stand alone memory element. This would suggest that a majority of the individual synapses within the brain may be independent memory elements. These synapses could be generated metabolically at any time and then switched electrically, within nanoseconds, to represent a data bit at any time. Depending on the bias conditions, the switching could result in a permanent change of state for these Zener diodes much like that involved in "burning a PROM" in computers.

The asynchronous nature of the signal processing within individual engines of the brain suggest considerable difficulty in perception because of the availability of important information at different times. Such variability in the assimilation of information accounts for many of the problems in judiciary proceedings related to eye witnesses and to many illusory and "magic" effects.

15.7.3.1 Critical importance of the thalamic reticular nucleus in vision EMPTY

15.7.3.2 Critical importance of limbic system in homeostasis EMPTY

15.7.4 Types of neurons

All of the characterizations of neurons within the brain found in the literature have been based on morphological (cytological) considerations (except for one still classified using the name of the man who described them). They have generally fallen into a grouping based on size of arborization field and occasionally on the number of arbors or their similarity to a simple shape such as a pyramid or star[151]. Based on this work, the so-called stellate cells appear to be related to the decoding of signals delivered by projection neurons. These cells are usually described as a subclass of the granular cells. Pyramid cells appear to be projection neurons that perform the encoding of the original signals. As in the case of the retina, horizontal cells appear to support short distance communications laterally within the plane of the neural surface. They are often shown in layer one of the laminate.

15.7.4.1 Neuron families based on function EMPTY

[xxx correlators, sample and hold, etc.

15.7.4.2 Neuron families based on morphology EMPTY

[xxx see names in Steriade brain slice book

15.7.5 Interconnections and signal velocities

The brain uses two major classes of interconnections. Over distances of less than two mm., all interconnections are carried out in analog mode between adjacent neurons using "gap junctions," i. e., active electrical interconnection devices. These devices are Activas used as diodes to provide optimal forward coupling, and negligible reverse coupling, in passive circuits used typically for signal summation.

The phase velocity of signals within the myelinated neurons is quite high, averaging 4,400 meters/sec over

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[151]Noback, C. (1967) Op. Cit. figure 16.3

distances of less than a millimeter. Thus travel times for a nominal myelinated neuron spacing of 10 microns is only 2.3 x 10^{-9} seconds or 2.3 nanoseconds. For unmyelinated axons, the velocity can be expected to be lower. However, the size of neurons can be considerably less than ten microns.

Because of the significance of capacitive loading related to small diameter axons, interconnections extending over two mm. normally involve signal encoding of the form used in stage 3 of the visual system. The encoding neuron is arranged as an astable, generally monostable, multivibrator. It generates action potentials in response to a stimulus. The axon of this multivibrator is long, myelinated, and frequently found to incorporate Nodes of Ranvier as signal regenerators. The myelination accounts for the white appearance of the majority of the neural pathways found interconnecting the engines of the brain.

Because of the time required by the action potential generation and regeneration process, the group velocity of signals projected between engines, and between distant locations within the same engine, is low. This velocity, dominated by the time required by the regeneration process, is typically 44 meters/sec. at 37°C (23 ms per meter). To travel a centimeter, the signal requires 230 microseconds (0.23 ms).

Nolte has provided a set of figures describing the major interconnecting pathways of the brain and several brief tables listing the inputs and outputs applicable to individual nuclei[152]. His figure 17.24 is particularly interesting in that it suggests graphically that there is a morphological symmetry in the major visual pathway between the LGN and Area 17. Although a fan related to the lower right quadrant of the visual field is labeled Meyer's Loop, a similar fan closer to Area 17 related to the upper right quadrant is not labeled.

15.7.6 Maximum operating frequency–need for cache memory

All of the available data located suggests that the brain exhibits a variety of signals. Action potentials and a variety of other rhythmic and recognizable waveforms are frequently recognized. It is common to find these waveforms described as in the presence of other background signals. These background signals are not normally characterized with respect to their frequency content. It is reasonable to expect the frequency content of these background signals are limited by the impedance characteristics of the test configuration and equipment.

Pending more precise characterization, that may require several years, it appears that individual processing circuits within the brain can operate at switching times determined by their impedance and their current carrying capacity. Asynchronous switching at nanosecond rates is probably typical for individual small neurons. This would suggest that each engine of the brain can handle a very large number of parallel binary operations at a maximum clock rate of near one gigahertz. By combining the engines of the entire human brain, a data manipulation rate comparable to one hundred or more gigahertz class man-made microprocessors operating in parallel is obtained.

The capability of the individual engines of the brain to operate at effective clock rates of a gigahertz while the interconnection circuits require microseconds to transmit the data between engines imposes the same problems on these engines as is encountered in similar man-made devices. There is an overwhelming requirement for local cache memory within each engine, and possibly within very localized areas of a each engine.

15.7.7 The "Jennifer Aniston neuron" in the medial temporal lobe

Recently, Quiroga and colleagues have reported that a single neuron in the medial temporal cortex was selectively activated by pictures of actress Jennifer Aniston[153]. It was not activated by pictures of other actresses, or actors, or by other kinds of images such as houses, scenery and objects. They also claim to have isolated neurons that were sensitive to pictures of actress Halle Berry and the Sydney Opera House.

Baars & Ramsoy discussed this report in order to put it in context (pages 89-91. "It is important to keep in mind, of course, that we are sampling just some out of billions of neurons. In all probability, there is a complex network of related neurons, and a lucky hit will reveal a Jennifer Aniston or Sydney Opera House fan." The researchers used the axonal firing rate of single neurons as the measure of activity. There was no discussion of the mode of signaling in this area of the brain or with respect to this neuron and any potential associated neurons (if the signaling was by word serial/bit parallel signaling). Baars & Ramsoy suggest the loss of the identified neuron would not inhibit the identification of Jennifer by this individual because of the number of associated neurons involved. They also note that on ethical grounds within the medical community "Single cell recordings

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[152]Nolte, J. (1999) Op. Cit. Chap. 16, 17 & 22

[153]Quiroga, R. Reddy, L Kreiman, G. Koch, C & Fried, I. (2005) Invariant visual representation by single neurons in the human brain *Nature* vol 435(7045), pp1102-1107

are only rarely possible in human subjects." Quiroga & Ramsoy did identify their subjects as "eight patients with pharmacologically intractable epilepsy who had been implanted with depth electrodes to localize the focus of seizure onset. For each patient, the placement of the depth electrodes, in combination with micro-wires, was determined exclusively by clinical criteria." "Stimuli were different pictures of individuals, animals, objects and landmark buildings presented for 1 s in pseudorandom order, six times each. An unpublished observation in our previous recordings was the sometimes surprising degree of invariance inherent in the neuron's (that is, unit's) firing behaviour." "A response was considered significant if it was larger than the mean plus 5 standard deviations (s.d.) of the baseline and had at least two spikes in the post-stimulus time interval considered (300–1,000 ms)." This is a very unusual criteria, requiring only two spikes (action potentials) without interpreting the temporal relationship between those spikes. "Responses started around 300 ms after stimulus onset and had mainly three non-exclusive patterns of activation (with about one-third of the cells having each type of response): the response disappeared with stimulus offset, 1 s after stimulus onset; it consisted of a rapid sequence of about 6 spikes (s.d. = 5) between 300 and 600 ms after stimulus onset; or it was prolonged and continued up to 1 s after stimulus offset." "Pictures of Jennifer Aniston elicited an average of 4.85 spikes (s.d. = 3.59) between 300 and 600 ms after stimulus onset. Notably, this unit was nearly silent during baseline (average of 0.02 spikes in a 700-ms pre-stimulus time window) and during the presentation of most other pictures."

In examining their data with regard to Halle Barry, "This unit was selectively activated by pictures of the actress Halle Berry as well as by a drawing of her (but not by other drawings; for example, picture no. 87). This unit was also activated by several pictures of Halle Berry dressed as Catwoman, her character in a recent film, but not by other images of Catwoman that were not her (data not shown). Notably, the unit was selectively activated by the letter string 'Halle Berry'. Such an invariant pattern of activation goes beyond common visual features of the different stimuli."

Ramsoy, Balslev & Paulson, writing in the same volume (page 485 and reproducing the same figure) noted the variety of poses of Jennifer that caused excitation of the same neuron. They assert, "This finding demonstrates an invariant, sparse and explicit neural code that may be important in turning visual percepts into memories."

> It appears clear from the above remarks, the stimulated neurons were associated with the internal code for "Jennifer aniston" and "Halle Barry" etc. but had nothing to do with the visual sensory modality, stage 4 information extraction associated with the figures of different orientation or with the actual steps in reading written text..

A followup article by Quiroga, Fried & Koch has also appeared[154]. They reiterated their findings related to Jennifer Aniston and then expanded on those remarks;

> "In another patient, a neuron in the hippocampus lit up at the sight of pictures of actress Halle Berry and even to her name written on the computer screen but responded to nothing else. Another neuron fired selectively to pictures of Oprah Winfrey and to her name written on the screen and spoken by a computer-synthesized voice. Yet another fired to pictures of Luke Skywalker and to his written and spoken name, and so on."

After providing the above paragraphs, they proceeded with a revisit to their earlier work;

> "For example, the day after finding the Jennifer Aniston neuron we repeated the experiment, now using many more pictures related to her, and found that the neuron also fired to Lisa Kudrow, a costar in the TV series Friends that catapulted both to fame. The neuron that responded to Luke Skywalker also fired to Yoda, another Jedi from Star Wars; another neuron fired to two basketball players; another to one of the authors (Quian Quiroga) of this article and other colleagues who interacted with the patient at U.C.L.A., and so on. Even then, one can still argue that these neurons are grandmother cells that are responding to broader concepts, namely, the two blond women from Friends, the Jedis from Star Wars, the basketball players, or the scientists doing experiments with the patient. This expanded definition turns the discussion of whether these neurons should be considered grandmother cells into a semantic issue."
>
> "Let us leave semantics aside for now and focus instead on a few critical aspects of these so-called

[154]Quiroga, R. Fried, I. & Koch, C. (2013) Brain cells for grandmother *Sci Am* vol 308(2), pp 30-35.

> Jennifer Aniston neurons. First, we found that the responses of each cell are quite selective-each fires to a small fraction of the pictures of celebrities, politicians, relatives, landmarks, and so on, presented to the patient. Second, each cell responds to multiple representations of a particular individual or place, regardless of specific visual features of the picture used. Indeed, a cell fires in a similar manner in response to different pictures of the same person and even to his or her written or spoken name. It is as if the neuron in its firing patterns tells us: "I know it is Jennifer Aniston, and it does not matter how you present her to me, whether in a red dress, in profile, as a written name or even when you call her name out loud." The neuron, then, seems to respond to the concept-to any representation of the thing itself. Thus, these neurons may be more appropriately called concept cells instead of grandmother cells. Concept cells may sometimes fire to more than one concept, but if they do, these concepts tend to be closely related."

Following the above remarks, they undertook an explanation of their theory concerning how the responses of the recognition process were stored in memory;

> "Neuroscientists ardently debate two alternative theories of how memories are encoded in the brain. One theory contends that the representation of a single memory-the image of Luke Skywalker, for instance-is stored as bits and pieces distributed across millions or perhaps billions of neurons. The alternative view, which has gained more scientific credibility in recent years, holds that a relatively few neurons, numbering in the thousands or perhaps even less, constitute a "sparse" representation of an image. Each of those neurons will switch on to the image of Luke, whether from a distance or close-up. Some but not all of the same group of neurons will also fire to the related image of Yoda. Similarly, a separate set of specific neurons activates when perceiving Jennifer Aniston."

They relied upon what they have labeled "concept cells." Their semantic model, no diagrams or schematics, does not qualify as a testable model at this time. They did not introduce any activity related to the subject comparing the perceived images to memories stored previously in order to perform a correlation and generate a "recognition" signal that might be associated with their concept cells.

This work would suggest a significantly more involved mechanism leading to recognition of a signature presented to the sensory modalities. See **Section 4.6.3.2**. Following a learning process involving what a target subject looks like (in the case of Quiroga et al., this process involved watching television programs in which the target appeared frequently), it appears one neuron of the subject was stimulated when this target appeared in the field of view of their foveola. The stimulated neuron related to the target with a high (but not 100%) probability. In the case of Jennifer Aniston and Lisa Kudrow, it would be valuable to compare their respective raster plots to determine if these plots suggest the probability of correct recognition.

The recognition of a target with an associated probability appears to be similar to the methodology developed by the IBM computer named Watson when responding to a question on the TV program, "Jeopardy."

15.7.7.1 Recognition/identification versus perception in the cortex

The Quiroga et al. papers provide additional critical information about the operation of stages 4 and/or 5. They have identified individual neurons, through a random experimental procedure, that are related to the *recognition* of a specific perception. The recognition, or identification, event goes beyond simple information extraction associated with an image. In the absence of training, the individual would not have recognized Jennifer Aniston or Halle Barry (lacking such training, I would not have recognized either of these people or their image). Thus, the time interval of 300 to 1,000 milliseconds used in their experiments is indicative of the time required for the recognition process. They only recorded a few action potentials resulting from their one second exposure of the subject to a given image. They noted;

> "Responses started around 300 ms after stimulus onset and had mainly three non-exclusive patterns of activation (with about one-third of the cells having each type of response):
> • the response disappeared with stimulus offset, 1 s after stimulus onset;
> • it consisted of a rapid sequence of about 6 spikes (s.d. = 5) between 300 and 600 ms after stimulus onset; or
> • it was prolonged and continued up to 1 s after stimulus offset.
>
> For this study, we calculated the responses in a time window between 300 and 1,000 ms after stimulus onset. In a few cases we also observed cells that responded selectively only after the image was removed from view (that is, after 1 s). These are not further analysed here."

Their figures 1a and 2a also contain small frames that appear to count the number of action potential pulses in 0.1

second bins collected from six data collection trials. The record of the data collection trials is of quite limited resolution in the paper. By dividing the number of pulses by the bin width, they report the rate of action potential generation during these one-tenth second intervals with a maximum scale height of 40 Hz. The recorded rates vary significantly during the one second exposure to the recognized images (possibly related to a confidence factor). They assert that their results are statistically significant based on a variety of statistical criteria relative to the quiescent pulse rate in the absence of any imagery. However, at the same time they note their standard deviations related to a given set of recognized images approach numerically the mean value for that set of trials. **Figure 15.7.7-1** reproduces only frame **a** of their figure 1.

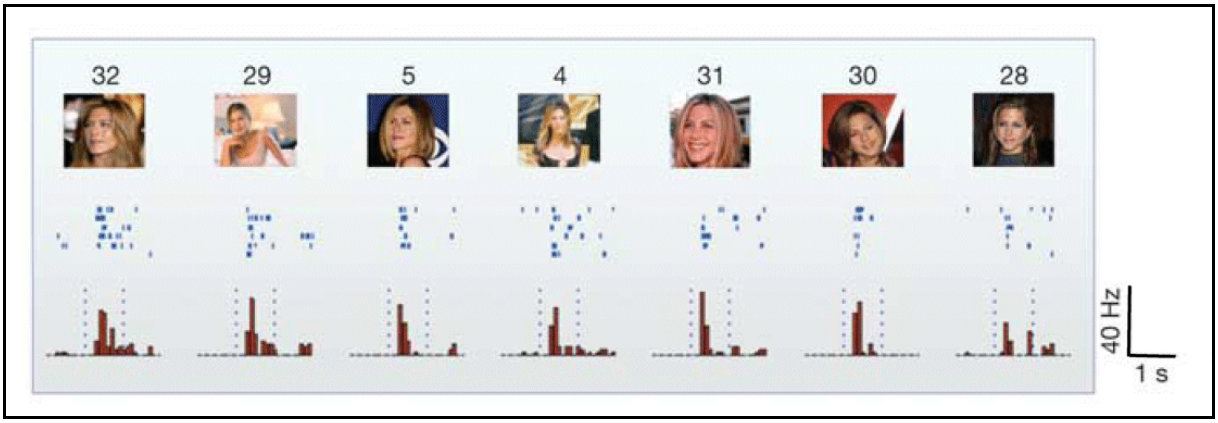

Figure 15.7.7-1 A single neuron recording resulting from 1 sec. exposures to Jennifer Aniston images. Quiroga et al. noted in their caption, "Owing to insurmountable copyright problems, all original images were replaced in this and all subsequent figures by very similar ones (same subject, animal or building, similar pose, similar colour, line drawing, and so on)." The replacement iImages were obtained from Corbis and Photorazzi, with licensed rights to reproduce them in this paper and in the Supplementary Information. Middle row; raster plots resulting from the above image (the order of trial number is from top to bottom). Bottom; post stimulus time histograms. Vertical dashed lines indicate image onset and offset (1 s apart). From Quiroga et al., 2005.

In this work, the initial delay of about 300 ms before the appearance of action potentials is indicative of the total signal processing time required to report a recognition. The pulse profile after that initial 300 ms may contain more information than described in the Quiroga et al. papers. Because of the initial 300 ms delay, it would be expected that the duration of the reporting signal would extend appreciably beyond the termination of the presented image. It is even reasonable to assume the reporting period is related to some form of short term memory persistence associated with the output of the stage 4 engines reported by the recorded neuron.

The temporal profile of the individual pulses associated with their raster scans may shed additional light on whether these pulses relate to a single word serial– bit serial stream or to a single bit in a word serial–bit parallel signal stream. The ramification of the temporal profile differ significantly between these two methods of signaling. There is even the potential that the neuron being interrogated is not the most significant bit in the case of a word serial-bit parallel format.

The papers imply the graphic images, text images and auditory messages presented to the subject are analyzed *en bloc*. However, this is not consistent with the operation of the neural system. As shown in other works by this author and highly annotated[155,156,157], each of these forms of stimulation involve a sequential operation by the neural system. The analyses are performed *en suite*. While the analyses of text images and auditory messages generally follow a procedure that is stylized to the point of being repeatable, this is not the case for graphic images. Each scan of each graphic image is likely to result in a significantly different signature. These considerations would strongly suggest;

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[155]Fulton, J. (2005) Processes in Biological Vision. http://neuronresearch.net/vision/pdf/7Dynamics.pdf Section 7.4.8, 7.5.2 & 7.5.3

[156]Fulton, J. (2005) Processes in Biological Vision. http://neuronresearch.net/vision/pdf/19Reading.pdf Section 19.8

[157]Fulton, J. (2006) Processes in Biological Hearing. http://neuronresearch.net/hearing/pdf/8Manipulation.pdf Section 8.1.4

• the scan patterns employed in analyzing the individual graphic and text images are not unique and
•the raster scans of Quiroga et al. are not repeatable at the detailed level because the neuron interrogated is not the most significant bit in a multiple word signature.

The raster scans of Quiroga et al. related to the text image of "Halley Berry" may be structurally different than those associated with her graphic images (indicative of a different analytical strategy within the neural system.

300 msec is not a long time in terms of neural processing. It would be most informative to obtain an MRI map from the test subjects involved and then record an MEG from these same individuals to obtain time correlated responses to when the earlier stage 4 information appeared in the illuminated parietal lobe area. Similar recordings from the occipital lobe would allow a determination of whether the process of recognition actually involved processing by the occiptial lobe or not.

15.8 The use of visual information by the limbic portion of the cognitive brain

Palermo & Rhodes have written a significant paper on the usage of information extracted by the stage 4 engines of the CNS by the limbic system. Aggregating the only figure in their paper with the hypotheses of this work provide a significantly clearer understanding of this interaction. **Figure 15.8.1-1** incorporates several modifications to add additional precision to their original. As they noted in their caption, the figure remains greatly simplified. Note the large number of bidirectional arrows in their figure. Many of these are not supported in this work (although like elsewhere, the *star network* form used in the CNS is recognized and accepted). The box labeled "Cortical Visual Areas" represent only the stage 5 visual areas of which at least two dozen individual engines have been identified out of an estimated 100 or more. Long dashed lines have been used to identify the engines associated with different stages of neural operation. The box labeled "Brainstem, Basal Ganglia," etc is a conglomerate of stage 4, 5 & 6engines.

The bidirectional path between the parietal lobe and the cortical visual areas has been separated into two separate paths, one from the re-labeled "Sensory (afferent) Parietal Cortex" to the stage 5 cortical circuits and one represented by the path from the cortical circuits to the motor (or efferent) portion of the parietal cortex represented here by only the "Premotor Motor Cortex (BA 6)" and the "Primary Motor Cortex (BA 4)."

Note the three unidirectional arrows at the right of the original. No source was described relative to these arrows. The three blue boxes at upper right are portions of the prefrontal lobe (within stage 5) of the CNS and share little common function with the engines of the parietal lobe (either the sensory (afferent) portion shown explicitly or the motor (efferent) portion shown in brief below the sensory portion.

Their label "Superior colliculus" along the dashed line from the retina is a very old label from early and relatively crude anatomy and histology. It is generally recognized that there is a bifurcation of the neurons in the optic nerve with a portion proceeding to the LGN and a second portion proceeding to an area along the histological brachia (branch) of the optic nerve proceeding to the superior colliculus. Anatomically, this area has been labeled the sensory portion of the SC, the medial portion of the SC or the Brachia of the SC. Functionally, it has been designated the perigeniculate nucleus (PGN) to more closely associate it with its functional cousin, the LGN.

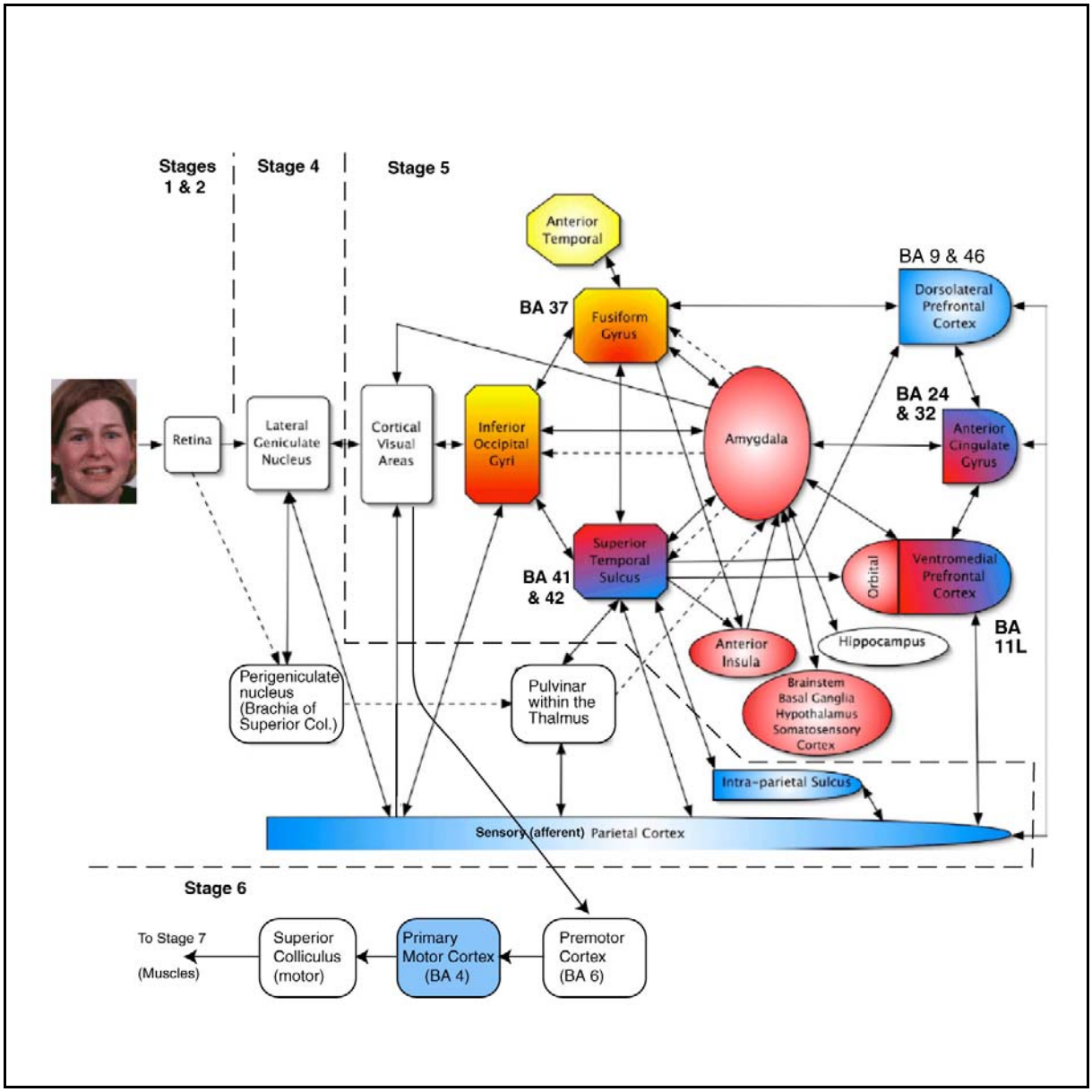

Figure 15.8.1-1 A traffic analysis of the limbic system of stage 5 reacting to stage 4 face recognition engines. Uncolored areas are external to the limbic system. Yellow areas are regions involved in interpreting the identity and semantic information from stage 4 under supervision of the non-conscious executive of the CNS. Red areas are regions involved in emotion analysis. Blue areas represent the foronto-parietal network involved in spatial attention. Solid lines indicate cortical pathways and dashed lines represent subcortical routes for rapid object recognition processing. Note the three unidirectional arrows at the right border of the original figure. See text. Modified significantly & reinterpreted from Palermo & Rhodes, 2007.

Palermo & Rhodes introduced their concept of two distinct visual paths as shown emerging from the retina. They related these paths to "fast" and "slow" brains in a more complex environment than appropriate. In their context, the slow brain is represented by the LGN-occipital pathway supporting the full retina. While this path is coarse in spatial resolution, it is not particularly "slow." It merely contains longer signal paths as required to reach the occipital lobe via the diencephalon, and return signals over similar distances to other portions of the diencephalon. It does address the entire field of view of the retina. On the other hand, the PGN-pulvinar pathway is the high spatial resolution portion of the system and it is more effectively placed within the CNS to

achieve early object recognition from only the 1.2 degree diameter portion of the foveola of the retina (centered on the point of fixation). The references to speed should be replaced by references to delay (or the commonly used but less precisely defined latency). Many investigators have noted that signals from the retina are frequently measured within the sensory portion of the parietal lobe before they are measured in the occipital lobe. The differences are due primarily to the physical distances involved and the velocity of stage 3 signal projection. Stage 3 signal projection is not shown explicitly in the figure but its impact is discussed extensively in **Chapter 9**.

Bullier has discussed the velocity of signal transmission within the CNS from a traffic analysis perspective[158]. He relied primarily on noninvasive event related potentials (ERP), also known as visually evoked potentials (VEP) and magnetoencephalography (MEG) data. Bullier did not distinguish between slow signals transmitted by *conduction* within a liquid or liquid-crystalline fluid and the much faster signals *propagated* by electro-magnetic waves over coaxial cables (myelinated axons). The difference in average velocity is on the order of 1:100, 0.4 m/sec for conduction and 44 m/sec for propagation. Bullier does discuss the use of these velocities in concept. Bullier did provide a table of latencies among elements of the CNS that is useful (**Section 15.6.7**).

Palermo & Rhodes identified three boxes with beveled corners (when four were shown) as the core system for face recognition. The work of others suggests these boxes are involved with *evaluation* of the information from the stage 4 engines of information extraction (the visual portions of the pulvinar and occipital lobe). They did not identify any functions directly associated with the general label “anterior temporal” at the tip of their figure. This and many other labels may have been adopted froma review by Haxby et al[159]. However, the labels used in their respective figures are distinctly different. The Haxby paper is relatively short and reports data for both the macaque and human subjects using primarily PET techniques collected during a series of investigations involving a variety of investigators. They summarize a set of outstanding questions on their page 231. In their Box 1, they ask and discuss, “Is the face perception system specialized solely for face perception?”

15.9 The extrapolation of biological vision to machine vision

Since the 1980's and specifically after the arrival of high capacity desk top computers that reduced the cost of computing to nominally zero, significant effort has been invested in the development of machine vision. The purpose has been to learn more about biological vision and to invent man-made equipment capable of emulating human vision.

A major problem has become buried in the foundation of machine vision research; the assumption that the biological vision modality employs integrating photoreceptors who accumulate the signal from a finite cross-sectional area photoreceptor. Based on this assumption, most of the machine vision research has come to depend on imagery acquired using a simple cyclopean (single optical path) camera to collect multiple frame imagery. This imagery has been used to support the integrating sensor concept. In the process, the machine vision research community has lost the capability to attack the stereographic capabilities of the visual modality.

As shown here, the visual modality employs change detectors in the biological retina that depend on tremor to emulate integrating type detectors while at the same time providing temporal information that allows stereographic information to be extracted from the bioptical capability of the two eyes.

15.9.1 Background of the machine vison approach to emulating biological vision

The machine vison community has not developed or relied upon a significant model of the biological vision modality. As a general rule, that community has ignored the role of the diencephalon and its components with regard to their critical role in understanding the vision modality. As of 2015, the machine vision community has not perceived the importance of the combination of an array of change detectors forming the retina and tremor providing a constant motion of the line of fixation and the external visual field in order to generate both a pseudo image of the external world while collecting and processing the time differences related to edge detection by the retina of the two eyes in order to capture the information necessary to acquire stereographic information about objects in the visual field.

With the omisson of the visual mechanisms described above, most machine vision models start with some version of a saliency map limited primarily to a 2D representation of the visual field (without any representation

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[158]Bullier, J. (2001) Integrated model of visual processing *Brain Res Rev* vol 36, pp 96-107

[159]Haxby, J. Hoffman, E. & Gobbini, M. (2000) The distributed human neural system for face perception *Trends Cogn Sci* vol 4(6), pp 223-233

of the high resolution foveola-PGN-pulvinar channel of information extraction in stage 4. This leads to their assumption that the low spatial resolution fovea– –occipital lobe path (omitting the LGN in the path) is the principle information extraction path in biological vision.

Papers appearing in the early 1980's can be taken as a beginning of the current machine vision school of computational modeling of the visual process. These papers are frequently described as biological vision-inspired with virtually no justification for this labeling. The inspiration frequently appears to have arisen from introductory textbooks suggesting the visual modality operates as a framing camera collecting a two-dimensional image of a scene. Marr introduced the concept of computational modeling of vision at the conceptual level prior to his untimely demise[160]. The 1986 paper by Canny[161] illustrates how the community was struggling at that time to discover how an imaging sensor array could provide a suitable edge detection mechanism so easily provided by an array of change detectors. To simplify his mathematics, Canny omits any description of the actual input signals obtained from a retina or imaging camera and assumes an image consisting of only parallel edges, thereby simplifying the problem to one dimension. He immediately introduces an distinct processing package directly behind the retina to perform complex mathematical computations including the evaluation of convolution integrals. The work does not proceed to a practical solution.

Itti et al[162]. provided a paper that ignores the role of the diencephalon in visual processing and conceptually connects the stage 1 imaging capability of the retina directly to a stage 4 saliency map in his figure 1. He does conceptually incorporate other stage 4 functions, such as surround differencing and a degree of scaling and normalization, prior to the saliency map. They cite two very conceptual models of the visual modality in introducing their figure 1. At one point they suggest the saliency map is located in either the parietal lobe of the cerebrum or in the pulvinar of the diencephalon. They do discuss information from the retina (as bottom-up signal flow) as well as information from the engines of stage 5 (as top-down instructions related to attention and prioritizing of areas in the field to be analyzed sequentially).

> "Input is provided in the form of static color images, usually digitized at 640 x 480 resolution. Nine spatial scales are created using dyadic Gaussian pyramids, which progressively low-pass filter and subsample the input image, yielding horizontal and vertical image-reduction factors ranging from 1:1 (scale zero) to 1:256 (scale eight) in eight octaves. Their figure 3 does illustrate how the biological vision modality does evaluate a scene sequentially based on targets uncovered by a low resolution image but they do not relate this image to the perifovea."

The time increments involved appear very long compared to those measured in actual vision (**Section 19.10.3**). They speak of a biologically plausible vision modality but do not describe their interpretation of plausibility.

> Since we do not model any top-down attentional component, the focus of attention (FOA) is a simple disk whose radius is fixed to one sixth of the smaller of the input image width or height. The time constants, conductances, and firing thresholds of the simulated neurons were chosen so that the FOA jumps from one salient location to the next in approximately 30–70 ms (simulated time), and that an attended area is inhibited for approximately 500–900 ms (Fig. 3), as has been observed psychophysically."

This quotation explains why the long time intervals in figure 3. These time intervals are used by the PEEP sequencing mechanism of this work (**Section 19.10,3**) to extract the information from their small fields of attention that are directly related to the foveola of the biological system (that is formally omitted from their model but represented by yellow circles and blacked out areas of the larger scene in their figure).

Their section 3.2 discusses the high spatial frequency associated with the rotation of the eyeballs acquired from eye-tracking data. This data confirms the presence of the PEEP sequencing mechanism.

Their conclusions are relevant to the machine vision challenge,

> "The type of performance which can be expected from this model critically depends on one factor: Only

---

[160]Marr, D. (1982) Vision. San Francisco, CA: W. H. Freeman

[161]Canny, J. (1986) A Computational Approach to Edge Detection *IEEE Trans Pattern Anal Mach Intel* vol 8(6), pp 679-698

[162]Itti, L. Koch, C. & Niebur, E. (1998) A Model of Saliency-Based Visual Attention for Rapid Scene Analysis *IEEE Trans Pattern Anal Mach Intel* vol 20(11), pp 1254-1259

> object features explicitly represented in at least one of the feature maps can lead to pop-out, that is, rapid detection independent of the number of distracting objects."

However, they note the massive data reduction calculations involved that are not likely to be employed in the biological equivalent of their machine vision model.

> In addition, at present, our model does not include any magnocellular motion channel, which is known to play a strong role in human saliency.

The paper also includes some useful analyses of identification via machine vision in the presence of noise that does not directly relate to biological vision.

A broader discussion of machine vision will be found in **Section 19.10.5**.

15.9.2 xxx Deviations between machine vison and biological vision

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(Inactive) DEFINITIONS INDEX (Use individual marks)

Principle of Univariance
Retinal illuminance
Transport delay
net photoreceptor