# Excerpts from

# The NEURONS and NEURAL SYSTEM

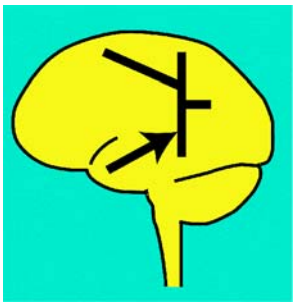
This material is excerpted from the full β-version of the text. The final printed version will be more concise due to further editing and economical constraints.

A Table of Contents and an index are located at the end of this paper.

A few citations have yet to be defined and are indicated by "xxx."

**James T. Fulton**
**Neural Concepts**

**jtfulton@neuronresearch.net**



April 28, 2021

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# 17 The Memory Elements of the Neural system[1]

[xxx see chapter 5 of Fuster, 3rd ed ]
[xxx draw up or copy a taxonomy of memory, Fuster pg 122 ]
[xxx perceptual versus executive memory [
[xxx perception action cycle ]
[xxx squire 1994 ]
[xxx lecture 7 from nottingham.ppt ]
xxx incorporate material from Rolls, E. & Deco, G. (2002) Computational Neuroscience of Vision. NY: Oxford Univ Press as presented in Chapter 4 in this chapter. ]

## 17.1 Introduction

The approach to defining memory differs greatly between the neuroscience and psychology communities. This has been highlighted in a recent text by Rudy[2]. Rudy used the left two columns of **Figure 17.1.1-1** to describe the activities of the psychology community and the neurobiology community. He noted the psychology community focused on the experience and behavior exclusively while the neurobiologist takes a broader view by looking at experience, brain systems, synapses and molecules leading to behavior. This was appropriate up through the end of the 20th Century. The situation has recently changed dramatically with the advent of the Electrolytic Theory of the Neuron (**Chapter 2** of this work). The still broader term neuroscience as used in the figure is meant to include all of the sciences that impact understanding of the neural system. Included in this column are electromagnetic propagation via Maxwell's Laws, coordinate chemistry as a broad field distinct from valence chemistry, and semiconductor physics applied to the liquid crystalline state of matter so ubiquitous (and dominant) in biology.

[1]Released: 28 April 2021

[2]Rudy, J. (2008) The Neurobiology of Learning and Memory. Sunderland, MA: Sinauer Assoc.

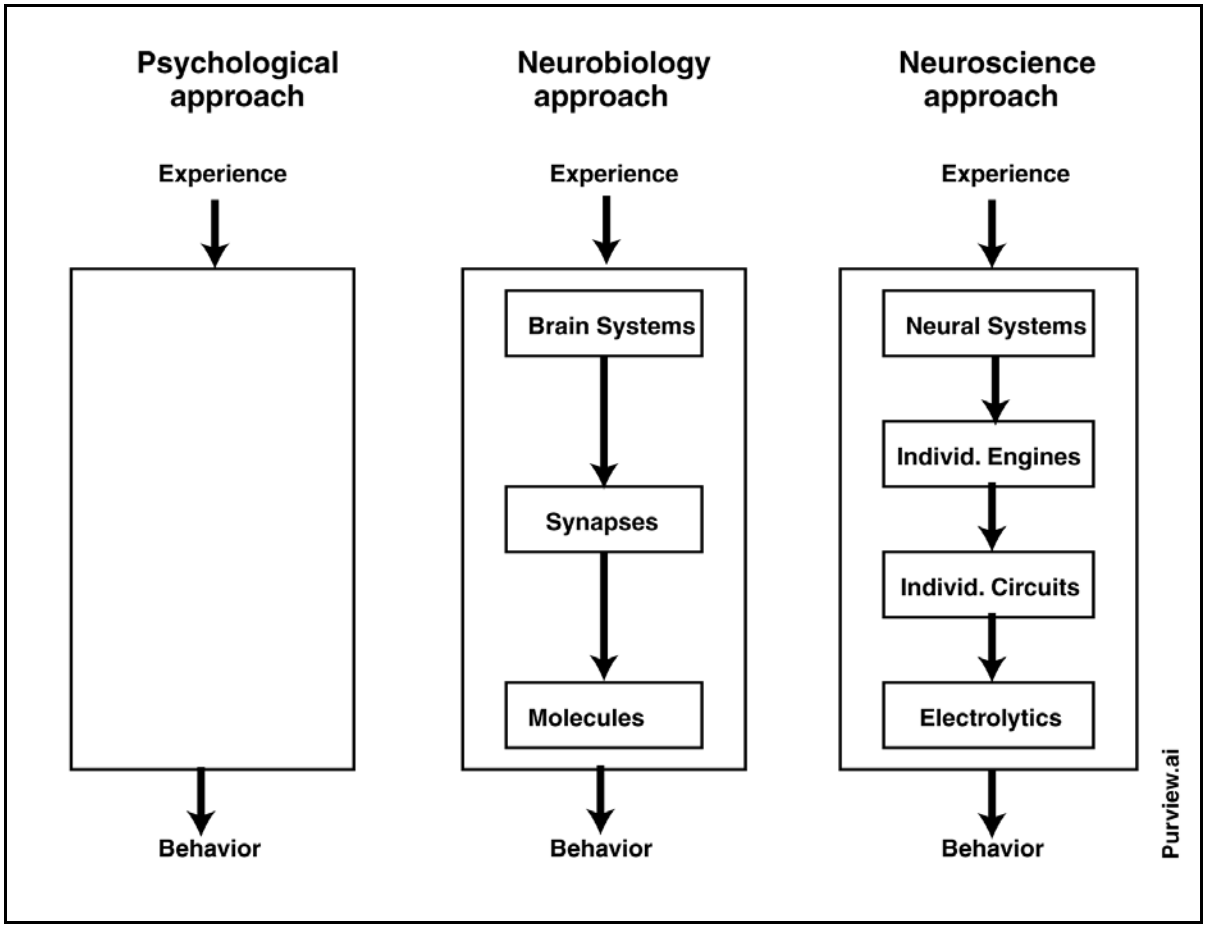


**Figure 17.1.1-1** The purview of psychology, neurobiology and neuro science. An extended understanding of the neural system based on its electrical performance under the Electrolytic Theory of the Neuron has occurred during the 21st Century. Extended from Rudy, 2008.

While psychologist's primarily speculated on what went on in the neural system until the advent of non-invasive imaging of in-vivo tissue, the neurobiologists took a broader view based primarily on cytoarchitecture, the synapses at the neuron/muscle junction, and the presumed molecular changes at those junctions (extrapolated to all neuron/neuron and neuron/glandular junctions. Unfortunately, these extensions were based primarily on the investigators primary education and not the strict scientific method. The primary education of the neurobiologist generally supported the implimentation of Bayes's Approach. The Bayes Approach, conceptually, draws up a list of expected results and implicitly excludes approaches not on the expected list. This approach limits the potential results to what one expected based on the investigators training and the current concepts in his community). ***The strict neuroscientific approach is to make no preconceived decisions concerning the outcome of an experiment.*** It places the historical record of findings by earlier investigators in their proper context.

Why Rudy limited the elements in his neurobiology cascade so severely is not obvious. Histology has indicated many other important elements within the neural system. This recognition began long ago with the separation of the central nervous system (the brain) from the peripheral nervous system. Similarly, while the synapse is present in the neural system, they are functionally only one class of critically important elements based on the active devices within the system. ***The fundamental active device is defined in this work as the 3-terminal active liquid-crystalline semiconductor device named the Activa.***

A stricter adherence to the scientific approach in recent times has led to a broader understanding of the neural

system as suggested by the right column of the figure. "Brain systems" is replaced by neural systems (including those external to the "brain." "Synapses" is expanded to include individual neural engines (typically containing several million neurons each and at least several hundred million synapses, ***and*** individual neural circuits created from electrolytic components including tissue, plasmas and the resulting active electrolytic devices. These neural circuits take on a variety of operating roles familiar to the electrical engineer but generally foreign to the neurobiologist. The individual circuits frequently display short term dynamic changes beyond the scope of conventional chemistry. All of these changes from the Rudy model are the result of the final box at lower right, electrolytics. Electrolytics, as used here, is the science of semiconducting devices in the liquid crystalline stage, generally employing coordinate chemistry (as opposed to valence chemistry) and heavily dependent on sterochemistry to impact the coordinate chemistry of many "reactions." Many coordinate chemistry reactions are at such a low energy level, that they are easily reversed without leaving any evidence that any reaction ever occurred. Much of the glandular mechanisms associated with the operating states of the neural system are dependent on the electrolytics described above, particularly the stereochemical bonding and coordinate chemical bonding of chemistry.

The dynamics of the neural system have been difficult for the neurobiology community to comprehend and document. State Diagrams, and other Servomechanism techniques, developed to a high art in the discipline of electrical engineering, are quite foreign to most investigators trained in chemistry or biology. Rudy has introduced elementary servoloops in his interpretation of the operation of the hippocampus and its associated engines in his chapters 10 & 11. Unfortunately in chapter 13, he frequently relapses back to double ended arrows connecting various neural engines when the underlying servomechanisms are clearly unidirectional. Learning in particular involves a a closed loop servomechanism of considerable sophistication. Learning is initially addressed in **Section 17.5** of this chapter.

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The psychologist, Fuster has enjoyed a long career in neural research focused on memory, primarily through observation of behavior – in both humans and monkeys. As the title and preface to his 1995 book emphasize, his premise at that time was that most memory centered on the cerebral cortex (alias, the neocortex or new cortex)[3]. "Thus, the scope of this book is broad but limited almost entirely to the neocortex, for the 'new cortex' is the seat of human experience and the focus of my research experience (page ix)."

> In the Introduction to the 1995 book, Fuster asserted, "This book is about the *memory of systems, not* about systems of memory. The distinction is crucial, for it clearly detaches the approach of this author from that of others who have explored the subject . . ." This author agrees *totally* with Fuster. The memory function is widely dispersed within the CNS. A memory module is associated with almost every engine of the CNS.
>
> *However, this work takes a broader approach.*
> - It recognizes the thalamus as of equal importance to the cerebral cortex. It also contains a variety of memory modules.
> - It also recognizes the distinctly separate cerebellum as containing a large number of independent engines with their own memory modules.

Fuster's recent (2003) book presents a more timely paradigm which he outlines carefully in his preface[4]. It continues his preposition that all memory is associated with the cerebral cortex (the cerebrum). He notes the previous work in the neurosciences has failed to yield causal relationships between mind and brain. He notes the recent and current progression from the modular model to a large-scale, widely distributed view of cortical cognition. He develops and explores seven "ideas" underpinning this new paradigm. It should be noted, Fuster's work does not involve study of the neuron and the actual neural system or how it exists in (forms) the central neural system. His only neural circuit diagrams are elementary block diagrams.

This work does not share Fuster's claim that all memory resides in the cerebrum. While much of memory may reside in the cerebrum, the cerebellum is an even larger storage site for memory and contains both more neurons and more synapses than the cerebrum. The obvious neurological role of the cerebellum and pulvinar

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[3]Fuster, J. (1995) Memory in the Cerebral Cortex. Cambridge, MA: MIT Press

[4]Fuster, J. (2003) Cortex and Mind: Unifying Cognition Cambridge, Eng: Oxford Univ Press

in memory is difficult to ignore, as required by Fuster's proposed paradigm. As is common among psychologists, Fuster defines a broad and largely overlapping range of memory types based entirely on behavioral and therefore primarily conscious studies. He does not explore the very large realm of learning and memory associated with the sensory and motor systems unrelated to cognition.

While Furster defines his terms much more precisely than is common in his field, the added precision introduces significant difficulties. His basis for organizing and discussion the books content (page 20) is the distinction between perceptual and motor memory. He defines perceptual memory (page 21) as "the knowledge of the world and of the self acquired through the senses. It includes the primary sensory qualities themselves, objects, events, facts and concepts." He differentiates perceptual memory from declarative memory. He defines motor memory as "including motor learning, motor skills, and classical conditioning." Unfortunately, he does not recognize the role of the superior colliculus or the cerebellum in motor skills memory. The role of these non-neocortex elements in motor memory is extremely well documented in the clinical literature. His motor aspects of the frontal lobe are generally limited to the pre-motor function by most investigators, with subsequent motor functions related to the cerebellum and superior colliculi acting as memory generally described as consisting of lookup tables.

His assertion that perceptual memory is focused on the frontal lobe and the motor memory is focused on the posterior cortex differs significantly from many other investigators and dismisses any role for the colliculi, the cerebellum and pulvinar in memory. In this work, his term perceptual memory is probably associated most closely with the saliency map (short term or scratch pad memory) and long term memory in general. It is yet to be shown that these types of memory are present within the frontal cortex.

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To better understand the role of memory as reported in the literature, several important steps need to be taken. 1) it needs to be more precisely delineated as to its various roles. 2) The QUESTION OF THE CENTURY needs to be answered. 3) The relationship between declarative memory and stage 5 cognition needs to be elucidated.

Step 1) is addressed beginning in **Section 17.1.2**. Step 2) is addressed beginning in **Section 17.1.1**. Step 3) is addressed beginning in **Section xxx**.

As noted in **Section 12.1**, this work is suggesting that the hippocampus, and the associated engines providing the storage and recall of declarative memory (as a minimum) may constitute a separate stage 5C Cognition Support (Memory) that is an integral element of the functioning stage 5 cognition. As developed in **Section 17.6**, it is the cerebellar cortex that is the primary location for the storage of memory, other than *current*, or working, memories being processed at various locations such as the saliency map.

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Fuster has restated Hebb's first and second postulates related to synapse formation in the context of memory. Hebb's postulates related to memory were similar to those of Cajal related to motor neuron operation.

Hebb's 1st Postulate– When an axon of cell A is near enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B is increased (Hebb, 1949, p. 62).

Hebb's 2nd Postulate– Any two cells or system of cells that are repeatedly active at the same time will tend to become 'associated,' so that activity in one facilitates activity in the others. . . [W]hat I am proposing is a possible basis of association of two afferent fibers of the same order–in principle, a sensory-sensory association (Hebb, 1949, p. 70).

Fuster then discusses the subsequent work of Marr and Stent related to these concepts. He notes, "There is no empirical evidence that two inputs must coincide precisely in time to produce effective association. (page 30)."

Fuster presents some useful graphics as part of his discussion of linguistics (Chapter 9).

Fuster notes an interesting relationship between what he calls perception and volition (page 294). In this work, the similarity is between the cognitive mode (the frontal lobe receiving information from short term,

scratch pad, memory) and the volition mode.(the frontal lobe sending information to the short term, scratch pad, memory for further processing).

Hawkins takes an opposite view from Furster, that is supported in this work. Hawkins observed (page 168) relative to the large brain structures, the basal ganglia, the cerebellum and the hippocampus, that lie under the cerebral cortex and communicate with it. "All three existed prior to the neocortex. With a very broad brush, we can say that the basal ganglia were the primitive motor system, the cerebellum learned precise timing relationships of events, and the hippocampus stored memories of specific events and places." Furster and Hawkins cannot both be right. Recent work has shown beyond question that at least a major part of memory resides in the hippocampus.

Hawkins[5]. takes a broad view of how the neocortex works His version can be extended to include the paleocortex and therefore the entire cortex. He notes the cortex in not like a computer, parallel or otherwise (page 68). Instead of computing answers to problems the cortex uses stored memories to solve problems and produce behavior.

- The cortex stores sequences of patterns.
- The cortex recalls patterns auto-associatively.
- The cortex stores patterns in an invariant form.
- The cortex stores patterns in a hierarchy.

The word sequence is important in the first Hawkins axiom. All memories are of this type. They consist of a concatenated series of individual memories that can be recalled beginning at any point in the sequence. He notes that it is virtually impossible to sing the song, "Over the Rainbow," backwards because the pieces of the song are stored in sequential memory.

Auto-associatively is extremely important in the second axiom. When you recall a specific aspect from memory, you are typically presented with a series of associated events to add context to the information recalled.

The fact that the information is stored in an invariant form is crucial in the third axiom. It is the feature that allows you to recognize a friend while looking at the back of his/her head or at a strange angle.

Hawkins also stressed the seriousness of a loss of hippocampal memory (page 169). "Without the hippocampus you can still talk, walk, see and hear, and for brief periods of time appear almost normal. But in fact, you are profoundly impaired: you can't remember anything new. Even if you met with your doctor five times a day for a year, each time would be like the first time."

Hawkins' assertion that the hippocampus sits at the top of the neural pyramid (page 123) is not supported here. He has lost perspective and proportion with respect to the hippocampus, the frontal lobe and the thalamus. He begins to explore this situation in "An alternate path up the heirarchy (page 171)," where he recognizes the critical role of the thalamus. His first example fails the reason test related to reading words (see **Chapter 19** in "**Processes in Biological Vision**"). This weakens his baseline case considerably. On page 174, Hawkins notes, "I have introduced many speculative ideas on how the neocortex works. I expect several of these ideas will prove to be wrong, and probably all of these ideas will be revised." The role of the hippocampus will surely be one of these.

Fuster has introduced more neural system imaging in Chapter 7 of the 4th edition of his long popular text[6]. He has described the material carefully but some readers may miss the fact that the figures are the result of "memory tasks" that frequently involve both sensory and motor aspects unrelated to memory. His segmentation of some of the data temporally is an effort to separate sensory, motor and memory aspects of the neural activity. However, in the context of this work, the neural system cannot be analyzed based on a single thread assumption. Neural signal processing is a highly parallel operation within stages 4, 5 & 6. Alarm mode and analytical mode activity frequently precedes general awareness activity by significant fractions of a second. The memory activity associated with the alarm and analytical activities may occur simultaneously

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[5]Hawkins, J. (2004) On Intelligence. NY: Times Books

[6]Fuster, J. (2008) the Prefrontal Cortex, 4th Ed. NY: Elsevier Chapter 7

with other subsequent activities. Memory activities should not be indiscriminately associated with every area that lights up in neuroimaging figures.

Fuster concludes (page 295), "There are very few solid facts from neuroimaging concerning the localization of specific working-memory content in lateral prefrontal cortex."

Buzsaki has prepared a significant book on the operation of the brain from the perspective of a non-invasive researcher relying upon MEG and now MRI techniques[7]. The book is a significant work and deserves more detailed analysis following the major discussion of this chapter (See **Section 17.7.xxx**).

Figure 5.1 in Buzsaki, reproduced as **Figure 17.1.1-2**, is important in understanding the terminology of the neurophysiologists involved in non-invasive signal recording. The signals labeled beta generally represent difference signals (such as those carrying color information) with a quiescent frequency in the 10-30 pps range. All of the classes found above 1.5 Hz can be associated with either stage 3 summing or differencing channels. The slower classes are typically the result of recording the cumulative electrical field from a great many stage 3 neurons performing different signaling functions without accounting for the difference in travel time between the individual stage 3 neurons and the location of the cumulative recording.

[7]Buzsaki, G. (2006) Rhythms of the Brain. Oxford Univ. Press

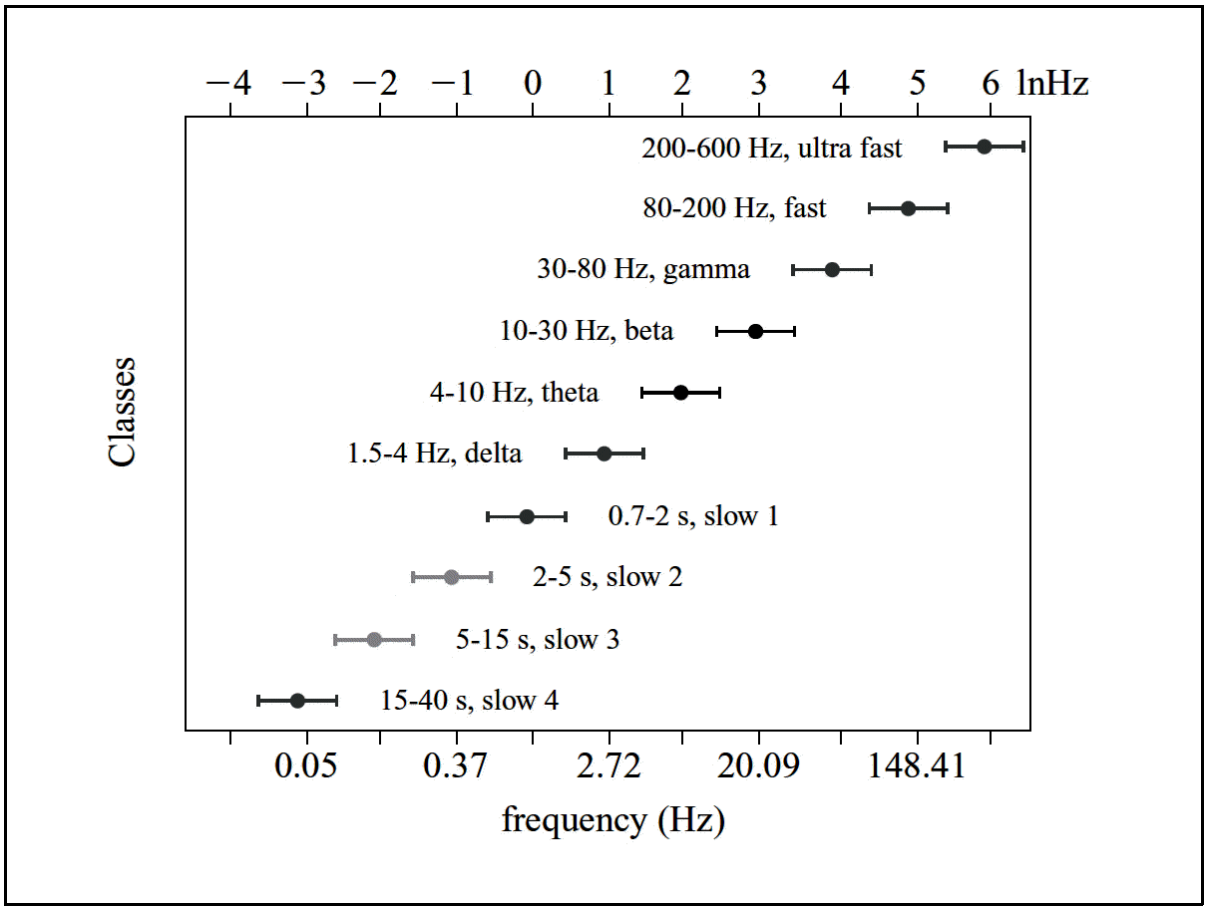


**Figure 17.1.1-2** Multiple oscillators form a hierarchical system in the cerebral cortex. Oscillatory classes in the cerebral cortex show a linear progression of the frequency classes on the log scale. In each class, the frequency ranges ("bandwidth") overlap with those of the neighboring classes so that frequency coverage is more than four orders of magnitude. Note the natural logarithmic scale at the top which accounts for the unusual scale at the bottom. Pulse frequencies in the 1.5 to 600 Hz range are normally associated with individual, or small groups of adjacent, stage 3 signal projection neurons. The lower frequencies are generally artifactual and due to the summation of the fields from a multitude of individual neurons. From Buzsaki, 2006

Squire & Kandel provided a coffee table book (including lovely painting on the cover) on memory in 2009[8]. It also included a intellectual exercise on the famous saying of Rene Descartes in the Preface. They discussed various conceptual anagams of "Cogito ergo sum,"—"I think therefore I am" while allowing for the translations from the Latin involved. The work reflects the conclusions drawn from a great deal of research into the workings of the CNS related to memory, based primarily on medical science and psychological investigations. Their only discussions on the operation of the brain are limited to the conventional chemical theory of the neural system. Many caricatures of the last 50 years are employed with only one or two electron micrographs.

> To establish a synapse, their position is that a very complex presynaptic specialization must develop that produces at least a handful of neurotransmitter related chemicals that are associated with a variety of pores in both the pre- and post synaptic structure, ***rather than*** the mere bringing into close physical contact, as required by the Electrolytic Theory of the Neuron, of the outer lemma of the pre- and post

[8]Squire, L. & Kandel, E. (2009) Memory: From Mind to Molecules, 2nd Ed. (2009) Greenwood Village, Colorado: Roberts & Co.

synaptic structures without the production or involvement of any new chemical chemicals related thereto or the introduction of any physical pores capable of transporting any ionic neurotransmitters!!

Their work describes a wide variety of memory modules and memory activities that will be addressed in the following material. Neither of these major presences in the neuroscience community have performed any fundamental research into the areas of neuroscience that they summarize, and particularly at the synaptic level. They have been principles in very well respected large organizations and supervised such research by large teams below them.

Squire & Kandel, 2nd Ed. will be reviewed in more depth in **Section 17.2.7**.

Kandel, Dudai & Mayford edited a substantial academic compilation of papers on "Learning & Memory" in 2016[9]. It focused on behavioral and psychophysical experiments attempting to reproduce and understand the large inventory of anecdotal information concerning memory. The original papers spanned a long time period and each paper includes an extensive bibliography. The Preface requires careful attention in order to understand what material might still be relevant. The word "magical" is used, apparently in the context of "something not understood by the uninitiated. The first paper by Squire & Dede includes two graphics that have appeared earlier (the first reproduced here with greater annotation in **Section 17.1.4**. The second appears in **Section 17.4**. These figures support their assertion, also supported here, "The notion of multiple memory systems is now widely accepted and establishes important organizing principle across species for investigations of the biology of memory."

## 17.1.1 THE QUESTION for this epoch in neuroscience

A great deal has been learned concerning the neural system during the last quarter of the 20th Century. The major remaining question concerns our knowledge of how and where declarative memory, in particular is stored. It has recently become clear that the hippocampus plays a major role in the formation and probably recall of declarative memory. However, what remains virtually totally unknown is where it is stored and how it is stored?. Two critical fundamental are; is memory stored in a straight forward spatial location, or is it stored in holographic form? ***and*** What coding form is used to store memory?

A careful traffic analysis of the neurons emanating from the hippocampus, and possibly leading to the hippocampus could be immensely enlightening. Are these neurons generated in sets of parallel neurons, an individual fascicule? What is the least common denominator in these fascicules? The mean of this least common denominator distribution could provide the number of bits in each word of the code (a serial word/parallel bit code).

With the code employed in the individual fascicules, the feasibility of discovering the spatial format used to store the code would be greatly facilitated. THE ANSWERS to these questions would take our understanding of how the brain works a very long way. These answers would provide an answer to this fundamental QUESTION for this epoch in neuroscience. It would move the question a long way from its current philosophical residence into that of harder science.

The Information technology age is just now entering the age of "BIG DATA." However, BIG DATA remains a small baby compared to the immense computational capability of one *Homo sapien* brain. With on the order of 100 billion neurons (half of which are within the cerebellum and roughly half within the cerebrum) and as many as 10,000 synapse interconnecting each neuron with a similar number of other neurons, the network complexity of the *Homo sapien* brain is beyond the ability of human researchers to comprehend. When one recognizes that the brain is fundamentally an asynchronous analog computer of such unlimited complexity, the repertoire of human researchers experience does not offer the fundamental tools needed for comprehending such a computational system.

Currently, the literature does not offer any support for understanding the operation of the animal brain beyond multiple *concepts* (primarily based on serial synchronous digital computer technology, even when "ganged" into large scale parallel computer suites *(ensuite* based on the French definition).

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[9]Kandel, E. Dudai, Y. & Mayford, M. (2016) Learning and Memory. NY: Cold Spring Harbor Laboratory Press.

## 10 Neurons & the Nervous System

Concepts, basically philosophical approaches, will not provide a handle on the actual character of the operating modes of the stage 5 cognition portion of the animal brain. A more fundamental approach is needed. How are abstract analog representations of the environment stored in declarative memory? How are abstract analog representation of the prior experience of the physiology of a given member of a species stored in non-declarative memory? These two forms of memory need not be stored within the same, or similar, physical entities. Neither need they be stored based on the same neural language. Humans have developed at least several hundred high level computer languages that can be used on a conventional central processing unit, CPU, to more optimally satisfy a given computational requirement. The number of subordinate languages operating on the same CPU/high-level-language configuration are endless.

### 17.1.1.1 Defining a program to attack THE QUESTION of the epoch

A serious research program, freed from any influence or association with concept of digital computers (except as a data collection medium), needs to be implemented to answer these questions (even in the presence of ever expanding capabilities within the domain occupied by suites of synchronous digital computer). A key methodology will involve multiple simultaneous probes accessing analog neural tissue, even when that tissue may be stimulated by stage 3 signal projection neurons delivering pulse coded information. The key will probably be to interrogate the smaller knots (ganglia) of neurons stimulated by the simpler fascicles of neurons capable of delivering word serial/bit parallel stimulation to that knot. An opportunity to make progress in this area may follow the work on olfactory glomeruli by the team led by Johnson & Leon at the University of California (Irvine) in the first quarter of the 21st Century. The number of independent variables involved in highly structured protocols investigating olfaction can be kept small and surgical access to the glomeruli are compatible with in-vivo experiments with animals.

Artificial intelligence, AI, is proceeding down a path that cannot be allowed to influence the above protocol development. It is totally reliant of synchronous digital computer, individually or *en suite*, to meet its goals.

### 17.1.2 Framework of memory in the neural system

The terms associated with memory in the psychology literature lack a framework. They generally reflect the context of the experiments of individual investigators. Memories take on a wide variety of forms within the neurological system. Eriksson has recently defined a mixed set of memory types along with their proposed primary locations[10]. A taxonomy of memory is necessary to understand the wide range of memories described in the literature, frequently without formal definition. **Figure 17.1.2-1** presents a framework for discussing memory.

Neurological memory can be separated into two major forms; declaratory memory which is accessible by the conscious mind and non-declaratory memory. Declaratory memory is frequently called explicit memory. The high level information stored in declaratory memory consists of cognits in this work. The variation in degree of accessibility of the cognits leads to the definition of a subordinate class of consciousness, described as the subconscious state. Declarative memory can be accessed from the subconscious mind with appropriate cues or pharmacology.

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[10]Eriksson, P. (2002) Nerve cells and memory *In* Ramachandran, V. *ed*. (2002) Encyclopedia of the Human Brain. San Diegeo, CA: Academic Press vol 3, page 309

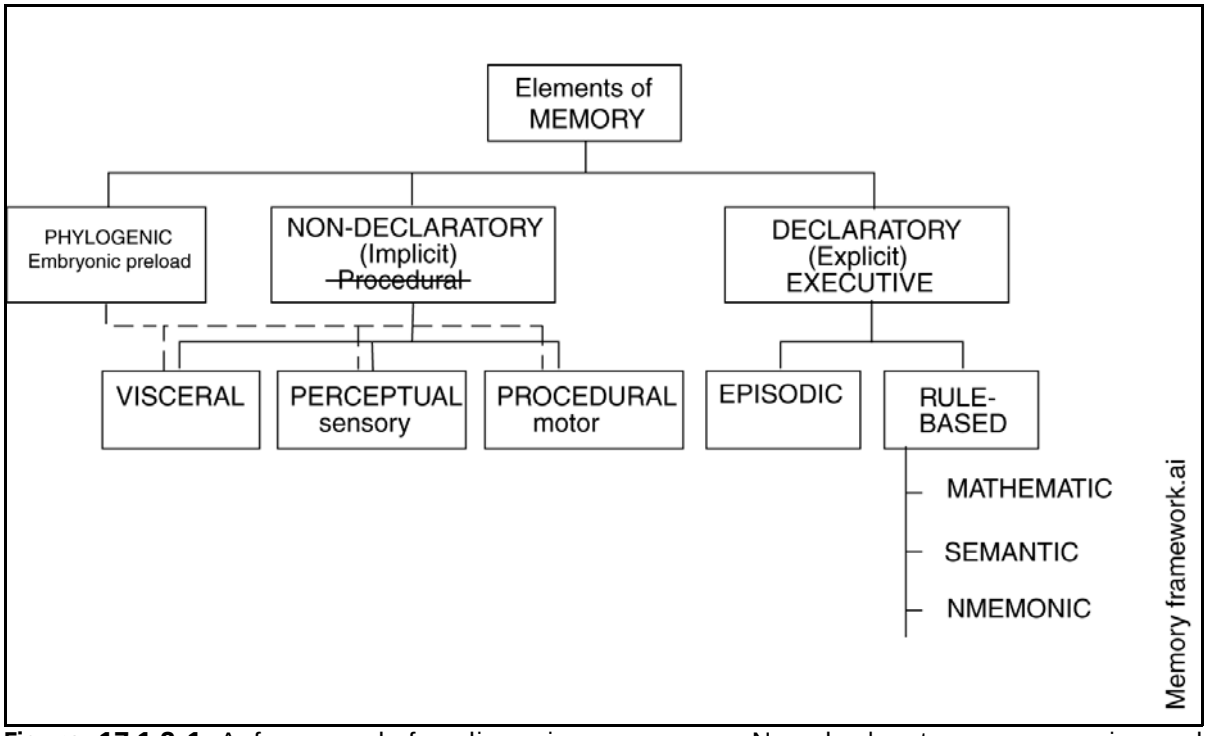


**Figure 17.1.2-1** A framework for discussing memory. Non-declaratory memory is used extensively throughout the neural system. There is clear evidence for a phylogenic preload of the memory system at birth. Declaratory memory may consist of a short term "working memory" along with permanent memory. Working memory appears to have a retention period typically measured in seconds. See text.

Non-declaratory memory is often called implicit memory. It is not accessible by the conscious mind under any circumstance. Therefore it is associated with the non-conscious state, or alternately the non-cognitive state(s) of the neural system. It can be subdivided into visceral, perceptual and motor memory. The information in non-declaratory memory is stored in the form of interps, percepts and other equivalent motor forms.

Squire & Knowlton have expanded the non-declaratory section of this figure to include many other types of non-procedural and non-perceptual learning identified psychologically[11]. [xxx expand on this in order to make the above figure more comprehensive. Be sure the cerebellum gets highlighted in some way ]

Ullman frequently identifies procedural memory as the counterpart of declaratory memory[12]. However, his studies are primarily concerned with the motor portion of non-declaratory memory in the context of language. Accordingly, he does not provide a conceptual space for visceral and perceptual memory components of non-declaratory memory. He discusses his definition of procedural memory in his section 3.2. Procedural memory is a synonym for the motor portion of non-declaratory memory in this work.

Ullman and his colleagues have written extensively on a declaratory/procedural (DP) model of the human

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[11]Squire, L. & Knowlton, B. (2000) The medial temporal lobe, the hippocampus, and the memory systems of the brain *In* Gazzaniga, M. *ed*. The New Cognitive Neurosciences, **2nd** Ed. Cambridge, MA: MIT Press

[12]Ullman, M. (2004) Contributions of memory circuits to language: the declarative/procedural model *Cognition* vol. 92, pp 231-270

brain. "The basic claim of the DP model: the brain systems which subserve declarative and procedural memory play analogous roles in language as in their non-language functions." The writings are dominated by text, with few or no graphics. The cited paper does include a 13 page bibliography that is very useful. This work considers the generation of motor commands of phonology to be a subset of the broader procedural memory system, as supported by Ullman & Pierpont in the psychology community and expressed in their Procedural Deficit Hypothesis (PDH)[13]. The problems their PDH is attempting to solve will be addressed in Section xxx on neural deficits. That section will suggest a broader functional model of language production than assumed by Ullman & Pierpont.

Sun has discussed the loading of declaratory versus non-declaratory memory[14]. He relates "bottom-up" learning with the learning of procedural skills (a subset of non-declaratory memory) before the learning of explicit skills that are declarative. His "top-down" learning is the opposite, the learning of explicit information before mastering the associated procedural skills.

**Section 18.6.6.2** discusses a quasi-declaratory sector of memory that may serve the phenomenon of dreaming while sleeping. The results suggest two distinct sectors of declaratory memory, with a potentially poorly defined boundary between the two sectors.

Declaratory memory is the home of episodic memory, memory related to personal experience and associated with a spatial dimension and a temporal dimension. It is also the home of rule-based memory, generally the result of the education process. While frequently associated with semantic memory, it is not limited to that type. It is also the home of mathematical memory and mnemonic memory, memory incorporating its own cuing device.

Hepp has recently written a paper from the perspective of a mathematical physicist. He asserts without any support that there is a mathematical memory heavily involved in, and supported by, the learning process[15]. He inserts that hypothesis into his "toy model" containing a description of a simple model of the ocular motor system. See **Section 19.10.6** for a more sophisticated model supporting both the coarse (beneric scene) and fine (analytical) operation of the object recognition process. While the paper is heavily mathematics oriented, his model is largely semantic and conceptual when he builds his framework on the conceptual "Blue Brain" of Markram[16], Hepp's (MBB). While his text describes at least four figures, they do not appear in the published paper.

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Sheremata, Malcolm & Shomstein[17] have made the assertion that "visual short-term memory represents information in retinotopic, not spatiotopic coordinates." If correct, this suggests that visual short-term memory is found prior to integration of the extracted information regarding the scene into the saliency map (**Figure 19.10.6-1** in **Section 19.10.6**).

To complete the framework of neurological memory, it is necessary to recognize the existence of some information in memory at the time of birth. This information is typically discussed in terms of an embryonic preload (similar to the hard-wired code used to bootstrap a computer into full operation). This preload is often discussed as representing, or developed from, the phylogenic history of the species involved. It may involve

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[13]Ullman, M. & Pierpont, E. (2005) Specific language impairment is not specific to language: the procedural deficit hypothesis *Cortex,* vol 41, pp 399-433

[14]Sun, R. (2002) Duality of the Mind. Mahwah, NJ: Lawrence Erlbaum Assoc.

[15]Hepp, K. (2009) The eye of a mathematical physicist *J Stat Phys* vol 134, pp1033-1057

[16]Markram, H. (2006) The blue brain project *Nature Rev Neurosci* vol 7, pp 153-160

[17]Sheremata, S. Malcolm, G. & Shomstein, S. (2014) Visual short-term memory represents information in retinotopic, not spatiotopic coordinates *2014 OPAM Convention*, Long Beach, Calif.

information in perceptual form, motor form or visceral form.

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The difference between knowledge and memories is a subtle one at best. Several authors have attempted to distinguish between them.

**Knowledge–** A collection of facts and relationships between facts. It is timeless. It may be stored in many forms

**Memory, A–** (narrowly) A collection of facts and relationships between facts stored within a neural system. The memory may be stored for a short term (in rewritable memory) or stored for a long term.

Fuster makes the case, there are no new neurological memories, only updated memories beginning with the initial "phylogenic memory" installed genetically during embryogenesis. Without going into detail, he argues (page 112) a new percept is uninterpretable and therefore unencodable as a new memory in the absence of a related prior memory. [xxx analyze this in context of this work.

Memory exhibits a number of different dimensions leading to a broad range of discussion in different contexts.

**autobiographical memory–** A frequently but poorly defined form consisting of both episodic and semantic elements of memory personally associated with an individual.

Brand & Markowitsch discuss the properties of autobiographical memory, and several other types defined psychologically, but do not provide a convincing case for its independence of episodic and semantic memory[18]. Their figure shows it as a sub-category of both of these types of memory. Their logic suggests that autobiographical memory may be supported by a range of memory addresses rather than a discreet physical memory. In separate figures, they suggest two possible conceptual circuits for creating long term memory. Both involve the thalamus as an important element.

**phyletic memory–** memory associated with the phylogenic,development of the species
and frequently associated with the embryonic development and initial neural programming of the individual subject

**declarative memory–** all memories that are consciously accessible.

**Nmemonic memory–** memory associated with a device to aid in its recall

**Semantic memory–** the memory of meanings, understandings, and other concept-based knowledge unrelated to specific experiences

**Episodic memory–** the memory of events, times, places, associated emotions, and other conception-based knowledge in relation to an experience

**non-declarative memory–** memories that are not consciously available (perceptual memory, procedural memory…)

**explicit memory–** also known as declaratory memory. knowledge that can be consciously brought to mind and 'declared'.

**implicit memory–** also known as procedural memory

**procedural memory–** "knowing how to do a certain thing." long-term memory of skills and procedures, or

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[18]Brand, M. & Markowitsch, H. (2006) Memory processes and the orbitofrontal cortex *In* Zald, D. & Rauch, S. *eds.* The Orbitofrontal Cortex. Oxford: Oxford Univ Press. Chapter 11

"how to" knowledge

**emotional memory–** Some episodic memory may be so harsh, that the system attempts to obliterate details related to it, and to be on extra alert to avoid similar situations in the future.

The psychology community frequently uses the additional term,

**working memory–** Short-term memory contained within the concept of declaratory memory.

Ingram has presented a popular book describing the above terms in more precise but still common language[19]. His focus was on Alzheimer's Disease, its history, current understanding of its cause and progression, and the potential for a cure during the next few decades.

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This work supports four primary forms of memory associated with the functional organization of the neural system;

•**executive memory** associated with the cognitive function,
•**perceptual memory** associated with the afferent neural signals of the sensory modalities, and
•**motor memory** associated with the translation of executive instructions into individual efferent neural commands to a specific muscle or gland.
•**visceral memory** associated with the homeostasis of the subject

Only the executive memories associated with the cognitive function are usually considered conscious memories, or memories that can be recalled to conscious memory. It is the executive, of declaratory memory that is the usual subject of the psychology community.

The figure includes a preprogramming capability to load individual neural circuits during embryogenesis. The capability appears to exist for any and all types of memory at the circuit level. This preprogramming and the subsequent expansion of memory through learning appears very similar to the bootstrapping operation employed in current computer systems. The machine begins with a very meager "boot" routine that looks around to find what assets it has access to and how they operate. It then configures a rudimentary operating regime that it can use to expand the capability of the complete system. This expansion of memory from a very limited embryonic memory is compatible with, but adds a different perspective to Fuster's view (page 112) that there is "no such thing as a new memory."

Major memory consists of two major components; what is called declaratory memory that is recallable by the subject and can be expressed (declared) to the attentive psychologist or clinical worker, and non-declaratory memory in which the subject is unaware of its utilization, but an investigator can establish exists. These are respectively called explicit memory and implicit memory. Implicit memory is also occasionally called procedural memory but this use of the term is dying out in favor of an alternate usage, to describe the memory associated with the motor system..

## 17.1.2.1 Aspects of working and executive memory

With reference to the psychology community, the current version of the saliency map will be described as the working memory portion of declaratory memory; the long term memory database forms the majority of the declaratory memory (**Section 1.2.1** & **Section 15.1.1**).

Wolters & Raffone have provided a paper involving both memory and consciousness in a complex conceptual

[19]Ingram, J. (2016) The End of Memory. NY: St. Martin's Press

framework[20]. They describe a "working memory (WM), including a 'central executive'." "We suggest that WM is best described as a set of three interdependent functions which are implemented in the prefrontal cortex (PFC). These functions are maintenance, control of attention and integration." While providing a large number of citations, they provide only a greatly simplified block diagram of the PFC in relation to the overall CNS. Their terminology needs to be rationalized in terms of this discussion.

Yu et al. have provided an alternate definition[21], "Working memory (WM) refers to aspects of online cognition, such as monitoring, processing, and maintenance of information. Since Baddeley and Hitch (1974) first published a chapter on WM, many theories have been proposed. One of the most widely supported theories is the controlled attention theory of WM (Engle & Kane, 2004). The theory suggests that individuals with high working memory capacity (WMC) may have better control of attention in integrating information from different domain-specific subsystems."

When interpreted in the context of the emerging view of the schematic of the CNS {**Section 17.7**), working memory may include sections dedicated to supporting stage 5A logical cognition and stage 5B emotional cognition, OR separate distinct engines supporting these two stages.

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Declaratory memory is generally described using three terms. Episodic memory is memory of events that the subject participated in before forming a long term record of the event. This type of memory is initially short term but can be transferred to long term memory, using a mechanism that is subconscious or non-declaratory. Semantic memory is not uniformly defined in the literature. Frequently, semantic memory is memory associated with the use of language. Alternately, semantic memory is described as the memory describing the characteristics of objects. Considerable progress is being made in determining the location of memory associated with language, or its associated subconscious control mechanisms. Mnemonic memory is a category where mneumonic devices are used to recall memories that are otherwise episodic or semantic. The mnemonic device may involve rhyming, sequencing, cross-correlation of features, etc. Some psychologists prefer to consider episodic and semantic memory as forms of mnemonic memory. The relative dictionary entries do not help clarify this situation or support a more precise set of definitions.

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Episodic memory, semantic memory, and amnesia.
Squire LR, Zola SM.
Veterans Affairs Medical Center, San Diego, California 92161, USA.

Episodic memory and semantic memory are two types of declarative memory. There have been two principal views about how this distinction might be reflected in the organization of memory functions in the brain. One view, that episodic memory and semantic memory are both dependent on the integrity of medial temporal lobe and midline diencephalic structures, predicts that amnesic patients with medial temporal lobe/diencephalic damage should be proportionately impaired in both episodic and semantic memory. An alternative view is that the capacity for semantic memory is spared, or partially spared, in amnesia relative to episodic memory ability. This article reviews two kinds of relevant data: 1) case studies where amnesia has occurred early in childhood, before much of an individual's semantic knowledge has been acquired, and 2) experimental studies with amnesic patients of fact and event learning, remembering and knowing, and remote memory. The data provide no compelling support for the view that episodic and semantic memory are affected differently in medial temporal lobe/diencephalic amnesia. However, episodic and semantic memory may be dissociable in those amnesic patients who additionally have severe frontal lobe damage.

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[20]Wolters, G. & Faffone, A. (2008) Coherence and recurrency: maintenance, control and integration in working memory *Cogn Process* vol 9, pp 1–17

[21]Yu, J-C. Chang, T-Y & Yang, C-T. (2014) Working memory capacity predicts workload capacity Visual Cogn vol 22(8), pp 1046-1048

## 16 Neurons & the Nervous System

Semantic memory is memory that is knowledge, factual or conceptual. Here are some sentences that demonstrate semantic memory:

I know what a Dalmatian looks like.
I know that there are 50 states in the U.S.
I know the alphabet.
I have my doctor's phone number memorized.
With semantic memory, you may not remember where, when, or how you learned the information, you just know it.

- - - - -

Wikipedia– Semantic memory refers to the memory of meanings, understandings, and other concept-based knowledge unrelated to specific experiences. The conscious recollection of factual information and general knowledge about the world, generally thought to be independent of context and personal relevance.

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### 17.1.2.1.1 working memory updating and maintenance

Nyberg and Eriksson[22] have addressed the maintenance and updating of memory in 2016. Their discussion is useful as an overview of their thoughts but lacks details and schematics.

### 17.1.2.2 Memory described in the time domain

Short term memory– (STM), memory stored in the saliency map prepared by the TRN. This portion of memory is "over-writable" and is continually updated by the sensory modalities. With effort, some short-term memories can accessible to the executive system for several seconds but seldom for a major fraction of a minute.

The term "working memory" has recently found a place in the neuropsychological literature. LeDoux has diagramed working memory in the same role as the saliency map of this work in presenting "immediately present stimuli" for the benefit of the "immediate conscious experience[23]." In the context of this work, immediately present stimuli are not sensory inputs but the information extracted from those inputs by the signal manipulations of stage 4. Burgess & Bird have briefly discussed working memory[24]

[xxx say short term memory is replaced by working memory ala LeDoux in this work ]
In this work, "working memory" (WM) is synonymous with short term memory. The content of working memory are found in the saliency map of stage 4. However, it may be useful to consider a copy of selected portions of the saliency map being transferred into the comparators of stage 5 during cognition. This portion would be related to the current focus of "attention" of the subject at that time. This copied portion of the saliency map could correspond to the cognitive map of O'Keefe & Nadel[25].

Long term memory– (LTM) memory xxx

O'Keefe & Nadel describe their concept as follows, "a cognitive map is a representation that "permits an

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[22]Nyberg, L. & Eriksson, J. (2016) Working memory: Maintenance, updating and the realization of intentions *In* Kandel, E. Dudai, Y. & Mayford, M. *eds*. Learning and Memory. NY: Cold Spring Harbor Laboratory Press.

[23]LeDoux, J. (2000) The amygdala and emotion: a view through fear *In* Aggleton, J. *ed*. The Amygdala, 2nd Ed. NY: Oxford Press pg 302

[24]Burgess, N. & Bird, C. (2009) Place cells indentify hippocampus with location-specific construction of mental images. *In* Mizumori, S. *ed*. Hippocampal Place Fields. NY: Oxford Press pp 156-157

[25]O'Keefe, J. & Nadel, L. (1978) The Hippocampus as a Cognitive Map. NY: Oxford Press

animal to locate itself in a familiar environment without reference to any specific sensory input, to go from one place to another independent of particular inputs (cues) or outputs (responses), and to link together conceptually parts of an environment which have never been experienced at the same time. This is a very broad description that requires additional expansion and specification in current contexts of the brain. It appears to incorporate elements involving the recall of long term memory, the focus of attention in response to immediate sensory inputs and the reprocessing of the saliency map to include new data, etc. Jeffery focuses on these additional aspects of the definition and reviews many similar definitions[26]. After noting that most of these definitions appear to involve the concept of a *relationships* between objects in the environment, she notes, "While this seems intuitively plausible, the difficulty is that *relationship* is a vague concept and the definition, in themselves, rarely specify strict criteria by which the existence of such a map may be proved or disproved."

The fourth edition of Fuster has used the term working memory extensively[27]. He has noted a "dualistic" concept of memory without further citation. He suggests its standing is fading in favor of a single unitary view of working memory. His definition of working memory remains largely conceptual, noting (page 4) that it "may be sensory, motor or mixed; it may consist of a reactivated perceptual memory or the motor memory of the act to be performed, or both." His definition of perceptual memory appears to be equivalent to current short term memory as developed in the posterior cerebral cortex, but without further definition as to its precise location.

In this work, it is clear that the "representation" of O'Keefe & Nadel is based on the information extracted from the sensory signals in stage 4. This representation includes the essence of the complete environment extracted currently and it is stored in the saliency map (the primary short term memory). These essences have nothing to do with the geometry or chemistry or pitch of the environment, they include only the features of the environment determined to be important by the organism through prior training and/or heredity.

> ***As an example***, a representation of O'Keefe & Nadel might be, I am in the presence of a friend, who is emotionally distressed, within a room familiar to me, in the evening; while simultaneously, I am in a calm and assertive mood and have prepared a response concerning the last communication from the friend, and am standing upright with my hand extended in friendship ready to speak at the appropriate instant. This representation does not involve any retinotopic, tonotopic or chemotopic characteristics. The information is entirely allocentric and abstract. Jeffery uses the term allocentric as synonymous with "world-centered." It could equally well be considered environment-centered. Alternately, it could be considered subject-centered in an inertial coordinate system.

The cognitive elements of stage 5 are free to examine the entire saliency map or to direct its attention to only elements of the saliency map.

[xxx edit the following ]

Definitions of **working memory** on the Web:

1.

memory for intermediate results that must be held during thinking
wordnetweb.princeton.edu/perl/webwn

Working memory (also referred to as short-term memory, depending on the specific theory) is a theoretical construct within cognitive psychology that refers to the structures and processes used for temporarily storing and manipulating information. ...
en.wikipedia.org/wiki/Working_memory

the memory system used for holding and manipulating information while various mental tasks are carried out. See articulatory loop.
homepage.ntlworld.com/vivian.c/Linguistics/LinguisticsGlossary.htm

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[26]Jeffery, K. (2008) The place cells–cognitive map or memory system In Mizumori, S. *ed*. Hippocampal Place Fields. NY: Oxford Press Chapter 4

[27]Fuster, J. (2008) The Prefrontal Cortex, 4th Ed. NY: Elsevier pg 4+

One well studied memory module that stores information needed for ongoing tasks over tens of seconds (such as a phone number). ...
www.klab.caltech.edu/~koch/glossary.html

Component of production rule system containing information that the system has gained about the problem thus far.
www.dbmi.columbia.edu/homepages/wandong/KR/krglossary.html

Short-term (recent) memory. See the entire definition of Working memory
www.emedicinehealth.com/attention_deficit_hyperactivity_disorder/glossary_em.htm

Ability to hold a small amount of material in memory for a short time while simultaneously processing the same or other material.
suffolk.edu/campuslife/11495.html

Sometimes also called `short term memory' by psychologists, it is a mental workspace consisting of a small set of data items representing the current state of knowledge of a system at any stage in the performance of a task, and which is transformed into a new set, in humans by the application of ...
www.cs.bham.ac.uk/research/projects/poplog/computers-and-thought/gloss/node1.html

Is also sometimes called short-term (recent) memory. Working memory is a system for temporarily storing and managing the information required to carry out complex cognitive tasks such as learning, reasoning, and comprehension. ...
www.brainrehab.org/NeuropsychTerms.html

A broad and multi-aspect memory class. In addition to a temporary store of information, it also performs manipulation of stored information ...
wps.pearsoned.co.uk/wps/media/objects/2784/2851009/glossary/glossary.html

Jeffery provides a lengthy discussion of the options related to working memory in the literature, including the rhetorical, “Might the Real Cognitive Map be Somewhere Else?” That discussion opens with, “A number of lines of evidence point to the possibility that the place cells are only one of several place representations in the brain.” In this statement, the term place as an adjective appears to be used in two different contexts. Place cells have been specifically identified histologically whereas place representations remain largely conceptual at this time.

**Long term memory–** (LTM), permanent memory where the information is transferred from short term memory under the control of the hippocampus.

### 17.1.2.2.1 Transfer of short term to long term memory

Brand & Markowitsch, writing chapter 11 in Zald & Rauch, have addressed the formation of long term memory largely in concept. Their perspective is slightly different from that of others exploring this relationship. They describe the orbitofrontal cortex as an element of the prefrontal cortex. They describe the steps related to memory in a different order than in this work (**Section 17.xxx**); Uptake, encoding, consolidation, storage and retrieval. They have defined several “dumbell” or “bottleneck” structures in their second paper of 2003[28] in order to help them identify these activities more clearly. They also provided an illustration, reproduced as **Figure 17.1.2-2**, to more clearly describe what types of memory they were discussing.

[28]Brand, M. Markowitsch, H. (2003) The Principle of Bottleneck Structures. *In* Kluwe, R. Lüer, G. Rösler, F. *eds* Principles of Learning and Memory. Birkhäuser, Basel

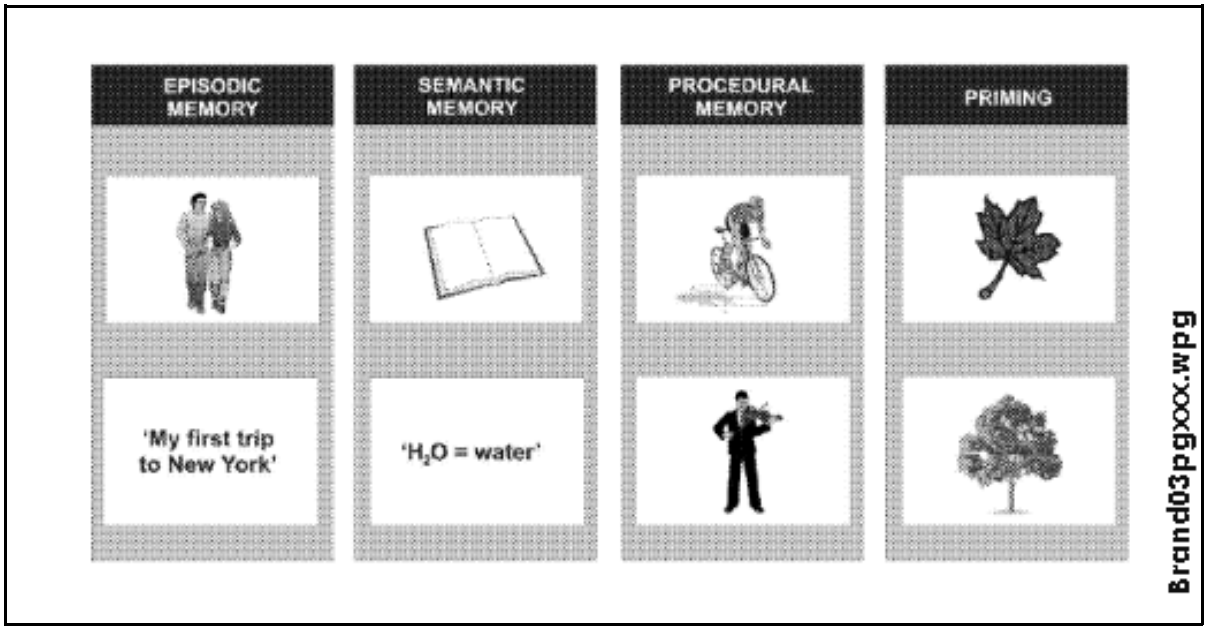


**Figure 17.1.2-2** Graphical description of types of memory ADD. Modified by Brand & Markowitsch in 2003 from Markowitsch, 1996.

Writing in 2006, they provided another set of examples of types of memory, to help clarify the above figure, **Figure 17.1.2-3**.

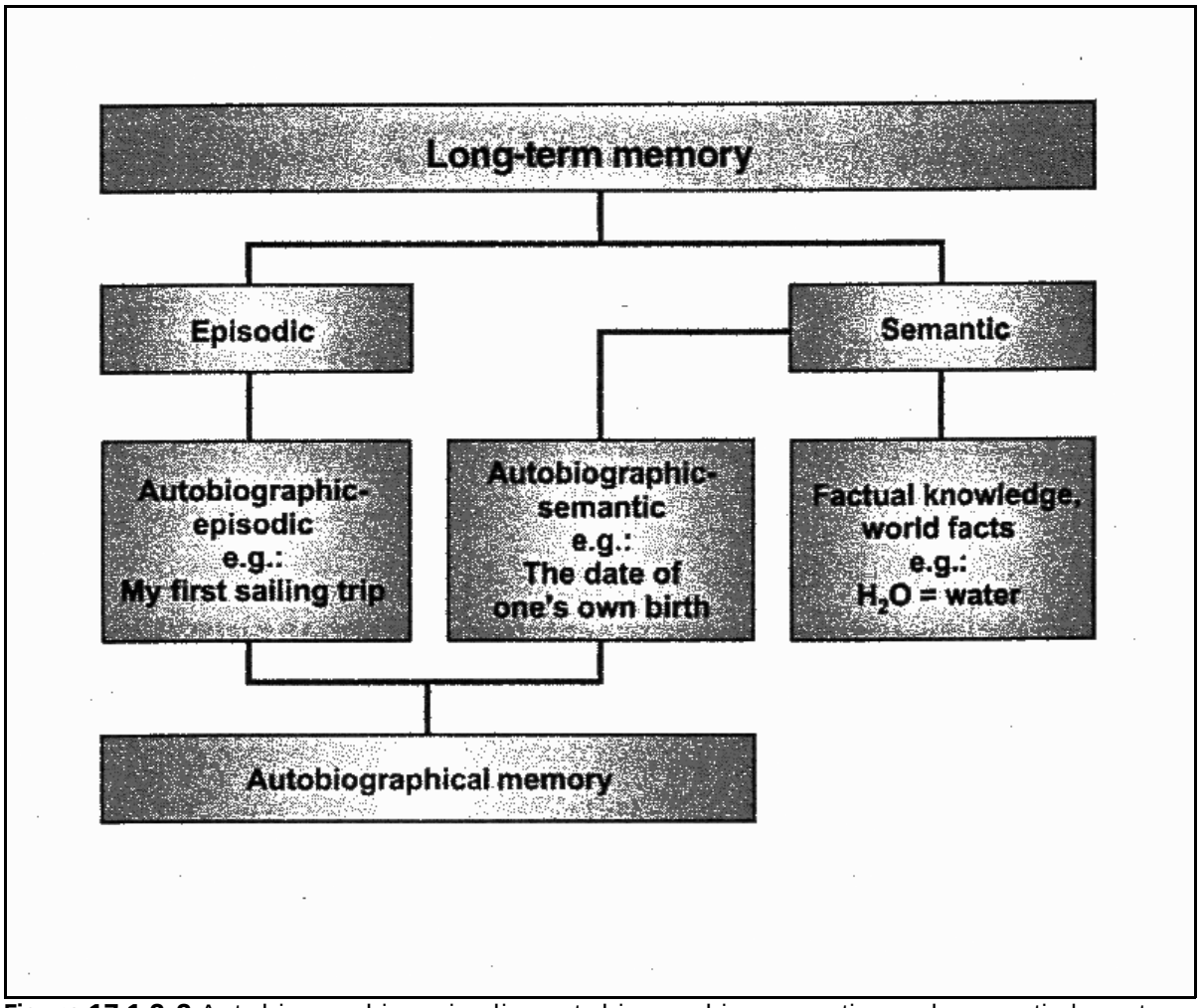


**Figure 17.1.2-3** Autobiographic-episodic, autobiographic-semantic, and semantic long-term memory. See theri text for details. From Brand & Markoitsch in Zald & Rauch, 2006.

Brand & Markowitsch define these bottleneck structures as "obligatory for reliable memory formation." They define two distinct paths for memory formation in their figure 11.2, reproduced here as **Figure 17.1.2-4**. [xxx add from Brand & Markow text. ]

The current Wikipedia (2017) asserts "the Papez circuit of frame (a) is a fundamental component of the limbic system. It is a closed neural circuitry that starts and ends in the hippocampus. It is also known as the medial limbic circuit. In 1937, James Papez proposed that the circuit connecting the hypothalamus to the limbic lobe was the basis for emotional experiences. Recent studies show that it has a more significant role in memory functions than in emotions. Some of the structures that Papez originally described such as the hippocampus now appear to have little to do with emotional behavior." "The Papez circuit involves various structures of the brain. It begins and ends with the hippocampus (or the hippocampal formation).

> *The Papez circuit is more a concept than a circuit*. It is clearly not a "minimal circuit" in the language of circuit design. The data of its formation is also indicative of its conceptual form. There has been much additional research the 1930's.

"Fiber dissection indicates that the average size of the circuit is 350 millimeters." Such a long loop undoubtedly involves some stage 3 signal propagation neurons. The presence of stage 3 signal propagation

neurons greatly influences the temporal parameter associated with the circuit.

"The Papez circuit goes through the following neural pathway: hippocampal formation (subiculum) → fornix → mammillary bodies → mammillothalamic tract → anterior thalamic nucleus → cingulum → entorhinal cortex → hippocampal formation."

"Various studies indicate that the Papez circuit is greatly influenced by the cerebellum and that perhaps the hippocampus is not the starting point of the circuit. Anatomically, this would make sense since the cerebellum is connected to the circuit with many fine fibers and fiber bundles." "The fornix is a bundle of nerve tracts made of white matter (stage 3 signal propagation neurons). It is crucial in normal cognitive functions. Harm to the fornix can result in amnesia." Brand & Markowitsch concur in the view that the amygdala is more important in shaping emotional responses and the Papez circuit is more related to memory (page 287). However, the asserted circular signaling loop associated with the Papez circuit is quite troubling. Where specifically are its nodes of input and output? It is likely the element labeled the anterior thalamus in frame (a) actually refers to the portion of the thalamic reticular nucleus, TRN, overlaying that portion of the thalamus. The TRN controls much of the switching and control of primarily sensory neurons as they are traveling between engines of major morphological features (**Section xxx**).

The element labeled "mediodorsal thalamus" in frame (b) of the figure may only be the TRN covering the thalamus at that location.

Guillery & Harting have published most recently on the TRN in relation to the thalamus[29]. Their figure 1 clearly shows areas of the TRN overlaying discrete regions of the thalamus. Ulrich et al. have discussed the TRN overlaying the thalamus of the prosimian primate *Galago*.[30] The terminology used in their figure 1 is unusual but clearly explained. They do not show the paths of individual neural fascicules from the optic tract, OT, as they terminate in individual layers of the lateral geniculate nucleus, LGN (**Section 4.6.2.2**).

Brand & Markowitsch, along with many other sources have asserted that "Patients with circumscribed damage of the amygdaloid structures often demonstrate particular deficiencies in forming emotional memory (page287). In contrast, the Papez circuit is now regarded to be broadly involved in information transfer from short term to long term stores (encoding and consolidation. Even very small lesions restricted to structures of the Papez circuit can result in severe anterograde memory impairments, involving an inability to learn new information."

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[29]Guillery, R.& Harting, J. (2003) Structure and Connections of the Thalamic Reticular Nucleus: Advancing Views over Half a Century *J Compar Neurol* vol 463, pp 360–371

[30]Uhlrich, D. Manning, K. & Feig, S. (2003) Laminar and Cellular Targets of Individual Thalamic Reticular Nucleus Axons in the Lateral Geniculate Nucleus in the Prosimian Primate Galago *J Compar Neurol* vol 458, pp 128-143

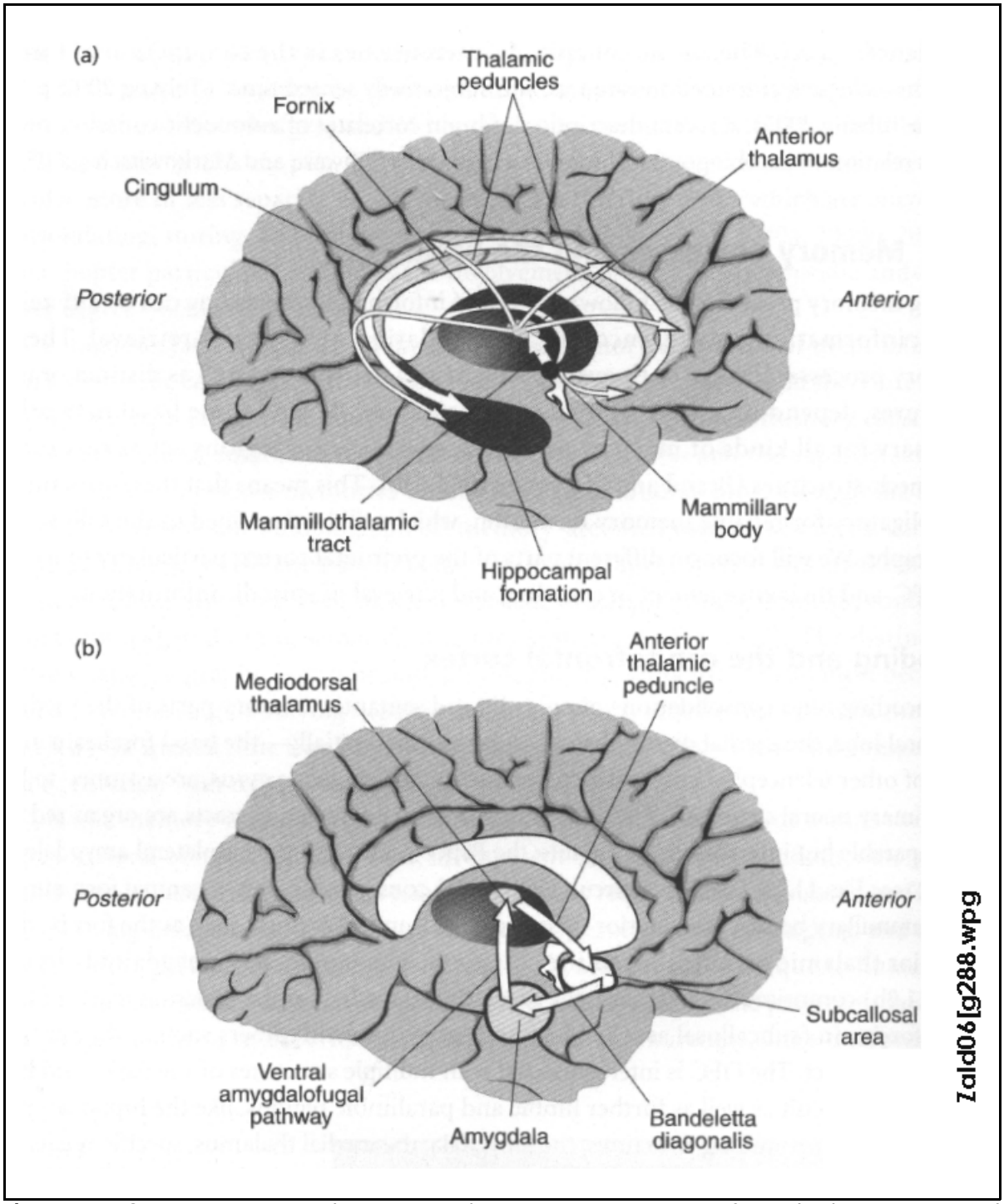


**Figure 17.1.2-4** Two separate short term to long term memory transfers. The interconnected circuits are engaged in the transfer of episodic (and partly semantic) information from short term to long term memory. In (a) the Papez circuit is presented; (b) represents the amygdaloid circuit. The element labeled "mediodorsal thalamus" may only be the thalamic reticular nucleus, TRN, covering the thalamus at that location. See text. Modified from Brand and Markowitsch, 2003)

### 17.1.2.3 Aspects of motor memory

Motor memory is best described as the lookup entries in the motor portion of the cerebellum that allows high level instructions from the cognitive portion of the neural system to be converted into detailed instructions addressed to a wide variety of muscles to ensure smooth and frequently complex motions of the overall skeletal system.

### 17.1.2.4 Aspects of perceptual memory

Perceptual memory is best described as the lookup table entries in the pulvinar and sensory portion of the cerebellum that support conversion of the individual sensory signals received at the CNS into information packets generally described as higher level percepts and sometimes described as cognits. Fuster (page 96) is less than precise, possibly due to the level of the object in the neural system, as to whether a cognit is a circuit associated with a specific piece of information, or is the piece of information that he also describes as a "symbol." In general, he appears to treat the cognit as a high level percept, or alternately symbol. The ability of higher level cognits to assemble and/or represent multiple lower level cognits suggests one group of higher level cognits are the entries into the saliency map of this work.

### 17.1.2.5 Aspects of visceral (limbic) memory

Thr area of limbic, emotional or visceral memory is becoming better understood as the subject of short-term memory and its loss. The loss of short-term memory as a major component of dementia and/or Alzheimer's Disease is becoming more important with each year. **Section 17.7** introduces the subject of limbic memory and its connection with long-term memory associated with the cerebellum.

## 17.1.3 Additional discussion of memory

While the operation of memory remains far from being understood, major progress has occurred in the last fifty years. A framework has begun to evolve that has provided significant, although still preliminary, answers about memory. A review by Milner, Squire & Kandel in 1998 is absolutely required reading if one is to understand where the field stood at the turn of the century[31]. The framework they review defines the type of memory of greatest interest in hearing as declarative memory. Declarative memory is associated with "knowing that" (the knowledge of abstract facts and events) as opposed to nondeclarative memory, the memory involved in "knowing how" (as in the knowledge of motor skills).

**Figure 17.1.3-1** shows the conceptual framework they established for discussing long-term memory. Their discussion also included short-term memory. Their discussion did not address the short term memory required in the operation (and particularly the information extraction functions) of the sensory systems. This type of memory would be associated with an expansion of the lower left of their figure, particularly the section labeled the diencephalon. The figure has been modified to highlight the additional relevant areas. Their label "medial temporal lobe" includes the hippocampal formation. The physiological portion of their discussion did not consider the electrolytic theory of the neuron presented in this work. Some of their diagrams (figures 7, 8 & 9) could be simplified considerably based on the electrolytic theory.

The definition of the medial temporal lobe in the above figure has not been standardized in the field of neuroscience. It frequently included the hippocampal formation. In some analyses[32], the hippocampus itself is thought to play a role in establishing sequences related to "knowing that" similar to the role of the cerebellum in "knowing how."

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[31]Milner, B. Squire, L. & Kandel, E. (1998) Cognitive Neuroscience and the study of memory *Neuron* vol 20, pp 445-468

[32]Fortin, N. Agster, K. & Eichenbaum, H. (2002) Critical role of the hippocampus in memory for sequences of events *Nature Neurosci* vol 5(5), pp 458-462

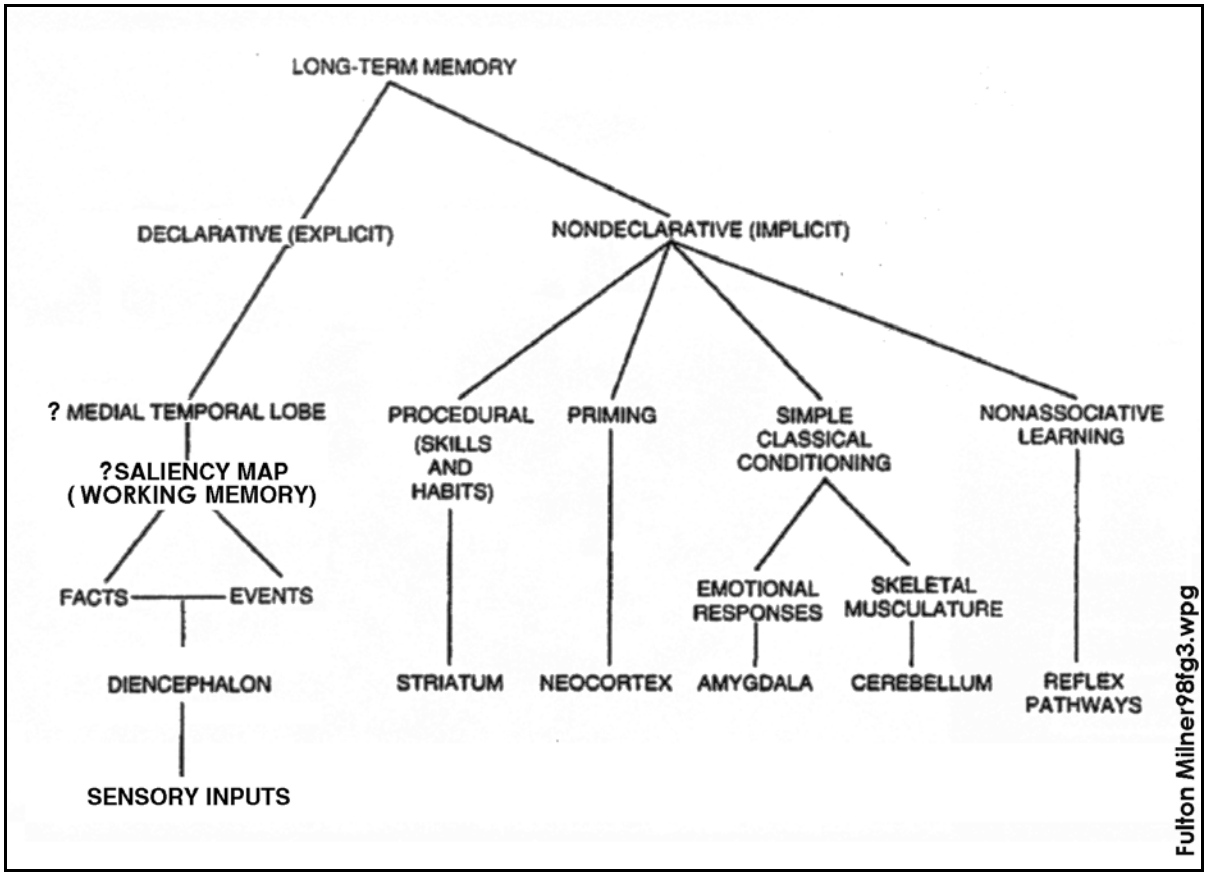


**Figure 17.1.3-1** Organization of mammalian long-term memory systems. This taxonomy lists the brain structures and connections thought to be especially important for each kind of declarative and non-declarative memory. The lower left of the figure has been expanded. The question marks note the uncertainty concerning the spatial centroid of these elements. No specific physical location is the primary element associated with the various types of memory; the names given tend to represent major engines mediating these types of memory. See text. Based on Milner, Squire & Kandel, 1998.

The role of the cerebellum in both declaratory and non-declaratory memory has been

strengthening in the 21st Century. However, the lack of knowledge concerning how memories are actually stored at the circuit level is hindering progress in this field. It is clear that information in topographic form is typically stored among the neurons of reticulated tissue. However, information stored in totaly abstract form may be stored in circuitry not yet recognized.

Burgess, Jeffery & O'Keefe have edited an excellent work providing significant data on the complex operations of both the parietal lobe and the hippocampus[33]. The editors are members of the anatomy community but appear to present considerable material gathered by the psychology community. The text provides no significant model or block diagram of these elements. However, it is clear that each of these morphological designations incorporate a wide variety of functional engines performing clearly disparate roles. The text describes the ongoing debate over whether the parietal lobe supports an egocentric or allocentric framework for sensory information without considering the possibility that a totally abstract database framework is used at that level within the neurological system. Burgess (page 11) asserts, "There are no direct projections from the hippocampus to the parietal cortex but there is an indirect projection which proceeds via the entorhinal cortex. . ." On page 19, Burgess suggests the perirhinal cortex may be the gating structure controlling the transfer of short term memory within the parietal lobe to the site of long term memory storage (**Section 8.2.3xxx**). Chapter 15 of the text provides more background on the organization of memory. The recent fMRI studies by Giovanello et al. confirm the role of the hippocampal formation in long term memory formation[34]. However, the resolution of the 3T MRI machine is not adequate to determine the role of the smaller elements such as the rhinal cortex.

## 17.1.3.1 The general requirements/features of the neurological memory

Kohonen has noted features of the memory system that make defining it a bit awkward, including the awkward relationship of the mind versus the brain. He noted, "One particular difficulty in the physical modeling of memory arises from the fact that the human mind, as a result of a long intellectual evolution, is able to deal with *concepts* that appear to be distinct and unique items, almost like material objects." This statement also applies to the perceptions of hearing. They can be treated like material objects. He continues, "The degree of specificity connected with the concepts is so high that very complex abstract structures of knowledge have been formed into our thinking."

Kohonen highlighted the important feature of associative memory and processing, the concept of content-addressing. In content addressing, the mechanism uses the content of a message to search a memory for other examples of that, or a similar, message. On page 3, he expanded on a paper by Aristotle on the observations on human memory which were later compiled as the Classical Law of Association." This Classical Law says:

> **The Classical Law of Association**
>
> Mental items (ideas, perceptions, sensations or feelings) are connected in memory under the following conditions:
>
> 1. If they occur simultaneously ("spatial contact").
> 2. If they occur in close succession ("temporal contact").
> 3. If they are similar.
> 4. If they are contrary.
>
> These remain the key features of the biological memory and recall system.

Kohonen develops this proposition further. He lists three significant features in the operation of a human associative memory: "(i) Information is in the first place searched from memory on the basis of some measure of *similarity* relating to the key pattern. (ii) Memory is able to store and recall representations as *structured sequences*. (iii) The recollections of information from memory in the most general sense are *dynamic*

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[33]Burgess, N. Jeffrey, K. & O'Keefe, J. (1999) The Hippocampal and Parietal Foundations of Spatial Cognition. Oxford: Oxford Univ. Press

[34]Giovanello, K. Schnyer, D. & Verfaellie, M. (2004) A critical role for the anterior hippocampus in relational memory: Evidence from an fMRI study *Hippocampus* vol 14, pp 5-8

*processes*, similar to the behaviour of many time-continuous physical systems." Finally, Kohonen noted, "Aristotle made several remarks on the recollection being a synthesis of memorized information, not necessarily identical to the original occurrences."

The above material appears to describe the critical memory portion shared by Stages 5 & 6 of the neurological system.

A distinction continually arises between short-term memory (STM) and long-term memory (LTM). The former is usually considered to involve a retention time measured in minutes at most while long-term memory is generally considered permanent (especially if immediate recall is not required). Hypnosis and merely day-dreaming can cause the recall of a great many events back to an early age, as far back as three years of age for uniquely significant events.

Experimental results are conflicting concerning the nature of long term memory (and probably the saliency map). Many investigators have concluded long term memory must be holographic in character since no specific area has been found that is dedicated to such memory. On the other hand, electrical stimulation of specific locations on the outer surface of the temporal lobe causes the recall of old memories. Repeated stimulation of the same location causes recall of the same memory.

## 17.1.3.1.1 The capacity of a holonomic memory

A feature of any holonomic memory is its ability to overlay multiple records on the same recording space. The individual records can be recovered by accessing the record holonomically from different positions, or at different scales, essentially without limit. In this context, the stored information is similar to that associated with multiple spread spectrum signals occupying the same radio frequency spectrum simultaneously. Unless, the receiver is listening with the same decoding algorithm, he only receives a low level noise like background. Kohonen has provided an example of the number of records that can be stored using a given array of neurons (pages 227-230). While highly idealized, it provides a perspective on what is possible. "Let us assume that a 'column' about 100 μm wide is regarded as one pattern element, whereby it contains about 500 neurons. If it is now assumed that each neuron has on the average some 5000 (modifiable) synaptic inputs, there would be more than $10^6$ inputs to such a 'group,' by which it can be encoded. This is then the parameter which roughly describes the number of linearly independent patterns, by which the 'group' can selectively be controlled. In other words, in a piece of network which consists of 'groups' of this kind, it is possible to superimpose over $10^6$ patterns in distributed form."

A critical feature of the holonomic method of storing information is the total inability of a laboratory investigator to probe for a specific piece of stored information at a specific location. The information relating to any event, present or past is stored in a distributed form. The situation is the same as for a holographic record. Globally, the record looks like a two-dimensional piece of film exposed to a noise source where one can occasionally observe some periodic wavy lines of limited extent[35]. Microscopically, every minute area looks like it contains a single grain of silver halide, or it doesn't. It is only when a finite area of the entire record is reconstructed through a transform that the original information is recovered. Until the transform used is determined, prospects for successful electrophysiological laboratory investigations of memory and cognition are distinctly limited.

## 17.1.3.1.2 An example of recall based on a content-address

**Figure 17.1.3-2** is a graphic example of the capability of an associative memory to use content-addressing[36]. A simple holographic form of holonom was used in this case. The image of the young girl was input to the optical system and stored on a reusable thermoplastic substrate in holographic form. The original source was removed and a fraction of the original image was input into the system to interrogate the stored image. As a result, the complete image was formed at the output aperture of the system (albeit at a lower performance level). The more complex holonomic concept allows additional dimensions of information to be stored in one record.

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[35]Pribram, K. (1981) Op. Cit. fig. 8-8

[36]Soffer, B. Dunning, G. et. al. (1986) Associative holographic memory with feedback using phase-conjugate mirrors *Opt Lett* vol 11, pp 118+

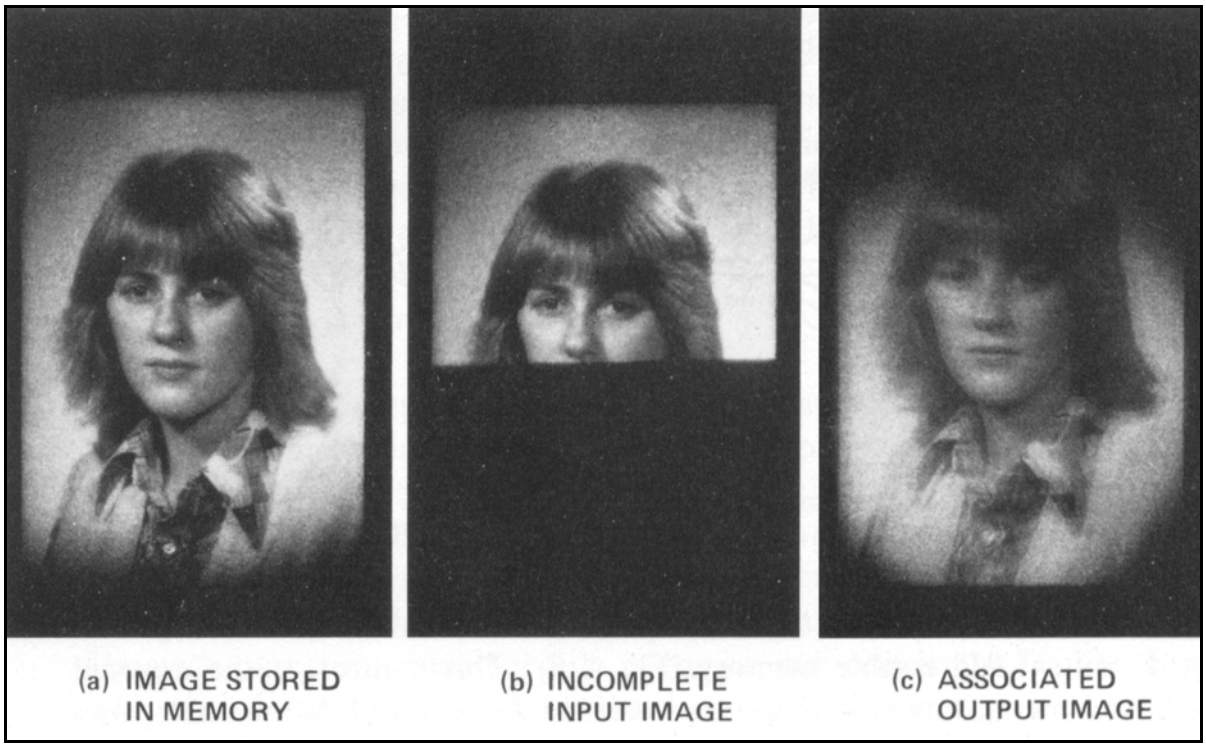


**Figure 17.1.3-2** An associative holographic memory system can retrieve full information even if only part of it is specified. The image was stored on an erasable medium. From Soffer, et. al, 1986.

The papers of both Pribram and Kohonen provide many insights into how an associative memory might be implemented but no clear physiological model. Imig & Adrain provided useful data in 1977 that relate to the work of Hubel et al. in vision[37].

## 17.1.3.2 The role of the Pons

[xxx This section is also reproduced in **Section 4.xxx** ]
While the pons has always played an important role in the architecture and morphology of the CNS, its specific functional role has not been extensively documented. This situation is changing in the 21st Century. The development of diffusion tensor imaging (DTI) from the earlier MRI technology has been a boon to the investigators of the cerebellum and its peduncles. It has provided details of this part of the *in-vivo* brain never available before. The result has been an explosion of academic reports in this area during the last ten years.

The Pons is acquiring the role of a large transfer point, particularly for the soma of a great many neurons traversing from one major portion of the CNS to another. Its role as described in **Figure 17.1.3-3** is that of a large "switch-yard," a term used widely in electrical power distribution. The switch-yard provides a central area where neurons from diverse sources can be routed to a variety of other terminal locations.

[37]Imig, T. & Adrian, H. (1977) Binaural columns in the primary field (A1) of cat auditory cortex *Brain Res.* vol. 138, pp 241-257

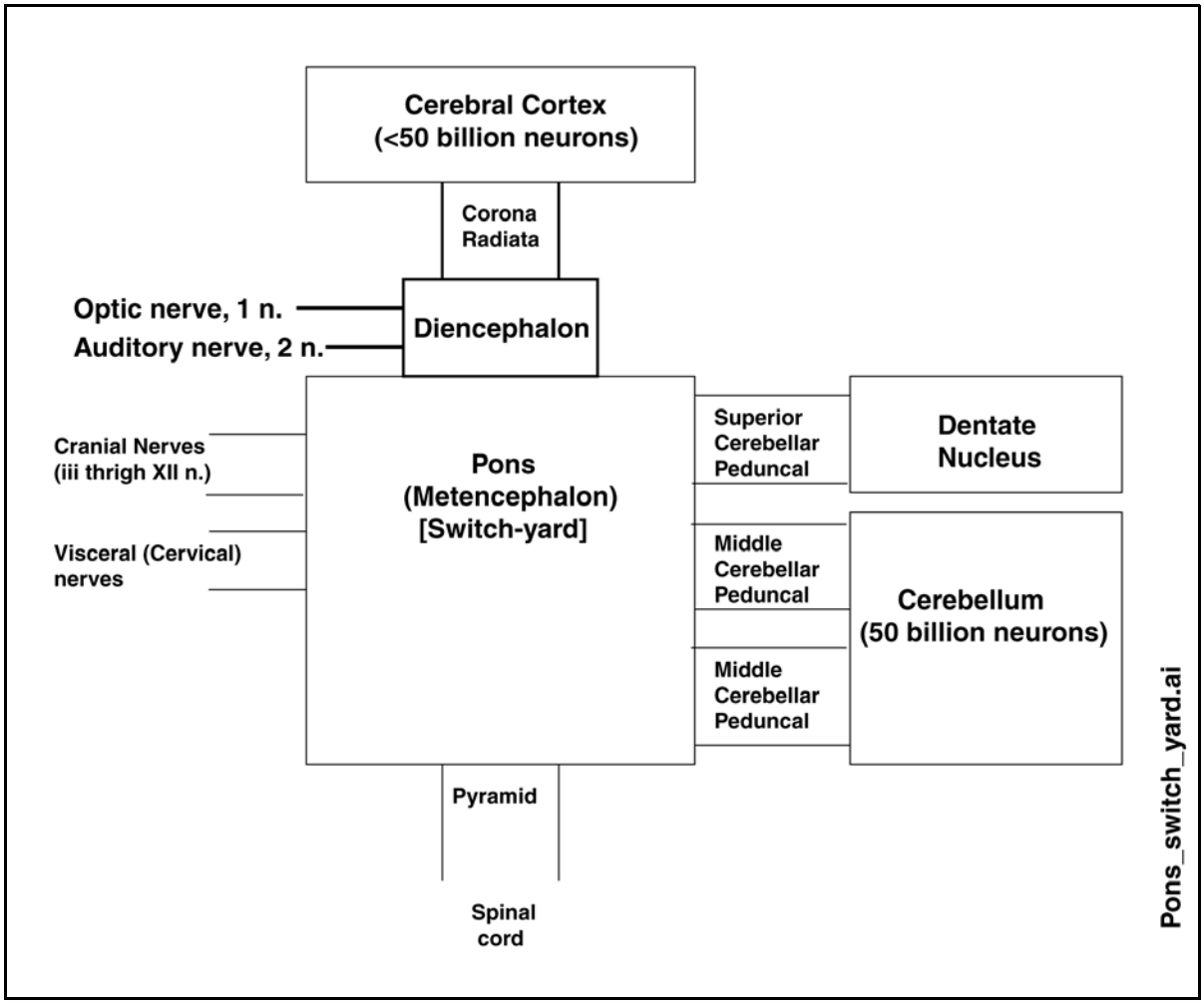


**Figure 17.1.3-3** Functional role of the Pons (the switch-yard or Metencephalon). The Pons is the dominant organ in the CNS by current neuron count, outnumbering the cerebral cortex by recent estimates. The importance of the role of the pons can be realized by noting the morphological dominance of the Peduncles (a.k.a. large brachia).

As Noback noted in 1967, "The boundaries between any two divisions of the brain stem are not defined precisely. The boundary between diencephalon and the mesencephalon is a plane passing through the posterior commissure and the caudal aspect of the mammillary bodies; that between the mesencephalon and the metencephalon is a plane passing caudal to the fourth cranial nerve and the rostral borde of the pons; that between the metencephalon and the myelencephalon is a plane passing eighth cranial nerve and the caudal border of the pons; and that between the myelencephalon and the spinal cord is roughly a transverse plane in the region between the caudal end of the twelfth cranial nerve and the first cervical nerve. . ." When the location of these elements varies on the order of millimeters in individual subjects, these boundaries obviously do not have great functional significance.

It would be useful to locate perimetry showing the size of the sum of all peduncles extending to the cerebellum compared to the Corpus callosum. It is likely the area of the peduncles is larger. It would also be useful using the new DTI technique of MRI imaging, to determine the percentage of neurons in each peduncle proceeding to the cerebellum, or the dentate nucleus, compared to the number exiting from these elements.

### 17.1.3.2.1 Background relating to the Pons

It would also be useful to show that the pons contains a great number of soma of individual neurons but virtually no pedicles of axons. Franklin[38] has noted in a 2017 compendium, "The middle cerebellar peduncles can clearly be seen passing from the pons to the cerebellum."
Habas & Cabanis[39] reported in 2007 on "Anatomical parcellation of the brainstem and cerebellar white matter: a preliminary probabilistic tractography study at 3." The number of images included is quite large. Catani & de Schotten[40] provided similar, but easier to visualize, material in a special issue of Cortex in 2008. Their Abstract notes,

> "Diffusion tensor imaging (DTI) tractography allows perform virtual dissections of white matter pathways in the living human brain. In 2002, Catani et al. published a method to reconstruct white matter pathways using a region of interest (ROI) approach. The method produced virtual representations of white matter tracts faithful to classical post-mortem descriptions but it required detailed a priori anatomical knowledge. Here, using the same approach, we provide a template to guide the delineation of ROIs for the reconstruction of the association, projection and commissural pathways of the living human brain. The template can be used for single case studies and case–control comparisons. An atlas of the 3D reconstructions of the single tracts is also provided as anatomical reference in the Montreal Neurological Institute (MNI) space."

The imagery provided is very useful.

### 17.1.3.2.2 The area of the cerebellar peduncles

The medical professionals have taken a considerable interest in measuring the shrinkages associated with the cerebellar peduncles in cases of Parkinson's Disease. The measurements are advancing with wider availability of high strength MRI machines.

Nicoletti et al. has provided some information on the width of the middle cerebellar peduncle width[41]. Their 14 control subjects had average middle cerebellar peduncle, MCP, widths of 9.80 mm ± 0.66, $P < .001$. Longoni et al. have provided more extensive data[42]. However, the medical investigators appear to focus on the width of the peduncles rather than their total area.

## 17.1.4 The location and means of memory storage

Science has yet to discover the code used to store memories within the neural system. This has made it more difficult to specify the location and means of memory storage. However, traffic analysis has made it relatively easy to determine the location of memory storage supporting the afferent and efferent neural systems. The mechanism of memory storage within stage 5 Cognition is yet to be addressed, much less described.

As noted in **Section 17.1.1**, the importance of the cerebellum in memory storage is advancing, especially when

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[38]Franklin, S. (2017) The Peripheral and Central Nervous System *in* Conn, P. *ed*, Conn's Translational Neuroscience. London: Academic Press

[39]Habas, C. & Cabanis, E. (2017) Anatomical parcellation of the brainstem and cerebellar white matter: a preliminary probabilistic tractography study at 3 T *Neuroradiology* vol 49, pp 849-863

[40]Catani, M. & de Schotten, M. (2008) A diffusion tensor imaging tractography atlas for virtual in vivo dissections *Cortex* vol 44, pp 1105-1132

[41]Nicoletti, G. Fera, F. Condino, F. Auteri, W. et al. (2006) MR Imaging of Middle Cerebellar Peduncle Width: Differentiation of Multiple System Atrophy from Parkinson Disease *Radiology* vol 239(3), pp

[42]Longoni, G. Agosta, F. Kostic, S. et al. (2011) MR Imaging of Middle Cerebellar Peduncle Width: Differentiation of Multiple System Atrophy from Parkinson Disease *Move Disorders* vol 26(2), pp 247-255

it is noted that the cerebellum contains a nominal 50%[43] of all of the neurons of the CNS (out of a current estimate of 100 billion neurons). The cerebellum is positioned so as to share stage 4 afferent and stage 6 efferent responsibilities under the supervision of both conscious and non-conscious stage 5 engines.

A recent article prepared for a popular audience describes the state of knowledge in 2013 concerning the location and character of memory in the human based on recent opportunities for "wiring the brain" in the management of epilepsy[44]. Quiroga et al. discuss the potential conceptual mechanisms for memory storage based on the very limited *in-vivo* data available. They do so from the perspective of a clinician and two computational neuroscience specialists. While discussing the potential "sparse" versus "distributed" form of memory storage, they do not precisely define these terms or recognize that distributed might mean storage involving many neurons in either a simple or holographic transform form of memory storage. At one point they do suggest the memory might be associative in character. Similarly, the term sparse is not used in the same sense as it frequently is in antenna theory and most mathematical treatises. Instead they use the term sparse to suggest a localized site for a specific memory of "grandmother." Such a site may involve a number of cells ranging from 10,000 to 100,000 (with an estimate of 18,000 by Lettvin in an earlier era remaining realistic). They note that "grandmother cells" may refer to cells that represent a "concept" related to grandmother rather than a specific representation of grandmother. Their general discussion is compatible with the architecture and morphology of the neural system developed in this work. However, all of their discussion is in terms of stage 3, action potential generating, neurons. They are apparently not aware of the analog character of the vast majority of neurons in the cerebral cortex.

More recently, discussions have surfaced suggesting that individual neurons might be exclusively associated with a given image; Section 15.7.7 of "Processes in Biological Vision," PBV, discusses the putative "Jennifer Aniston neuron."

### 17.1.4.1 The location of afferent and efferent memory storage

### 17.1.4.2 The location of executive (cognitive) memory storage

The trail related to how and where memory is stored in the neural system has become very vague at the posterior lobe frontal lobe interface, the Rolandic Fissure. While it is generally agreed there is little to no memory storage at discreet locations, there is great debate as to whether memory is stored "holistically" or "holonomically." The difference between these two terms may be more one of approach than fact. The holistic approach proposes the memories are stored using a relatively broadly based physical grouping of neurons. Fuster (page 112) suggests this grouping may be "an immense array of cortical networks or cognits that contain in their structural mesh the informational content." He goes on to assert, "Stored memories, like cognits, *are* cortical networks." However, there is an alternate interpretation that erases the boundary associated with the size of an immense array. The holonomic approach goes one step further and proposes memories are stored following a transformation into an information space that is not physically (spatially) identifiable (e.g., the waves of an optical hologram in Fourier space compared to the fixed spatial points of the decoded hologram). The holonomic approach is completely compatible with Fuster's thesis (page 116) that, "any neuron or group of neurons anywhere in a cognitive hierarchy can become part of many memories (emphasis in original)."

Employing the same networks of neurons in two different "real" domains is similar to the creation of phantom telephone circuits in man-made circuits. The use of individual power sources for each neuron does contribute to the feasibility of phantom circuits. However, extension of the phantom circuit concept to the same neuron participating in multiple domains becomes difficult. There is logic to converting over from a real to a synthetic domain for memory storage superimposed on an underlying functional network. More research is needed to answer the holistic versus holonomic question.

#### 17.1.4.2.1 Limbic or hippocampal short term memory

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[43]Shahruddin M. (as of 2017) xxx https://www.scribd.com/document/261024977/Cerebellum

[44]Quiroga, R. Fried, I. & Koch, C. (2013) Brain cells for grandmother *Scient. Amer* February, pp 31-35

While the location of executive memory storage remains highly controversial, there are a number of emerging facts.

1. The size of the cerebellum in terms of neuron count has changed dramatically. Recent studies by Herculano-Houzel has shown that in humans, it is over 75% of the total CNS neuron count (**Section 17.2.2.1**)

2. The hippocampus as the route to the cerebellum from the stage 5 cognitive engines, and the primary location of short-term memory storage is becoming more recognized.

These two facts are placing the cerebellum in line as the site of primary long-term memory storage. It is also emphasizing the role of short-term memory storage and as gatekeeper for long-term memory storage and recall within the cerebellum.

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## 17.1.4.3 The functional form of memory

Hebb described the formation of memory from an early perspective (1949)[45]. His insight, from a psychological perspective, was that;

> When an axon of cell A is near enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic changes takes place in one or both cells such that A's efficiency, as one of the cells firing B is increased (page 62).

By replacing the word firing with exciting, his insight remains valid today. The actual process appears to involve forming a new synapse as suggested by Hebb. Uttal's discussion of Hebb in a current context appears correct[46]. As suggested by this work, the "Hebbian synapse" is a conventional synapse involving the transfer of electrons across the junction, with the total area of the junction(s) defining the impedance of the junction. The formation of one or more new synapses as part of the formation of a new memory appears compatible with the formation of both declaratory and non-declaratory (procedural) memory. See also Fuster in **Section 17.1**.

Many investigators have speculated on the functional schematic of neural memory. Zipser et al. have described neural memory in the context of conventional electronic circuit memory technology and the concepts of Artificial Intelligence and neural networks prevalent in the 1990's[47]. They employed probabilistic neurons in feedback networks to emulate actual recorded neural patterns assumed to involve short term memory. No insight surfaced into the biophysical processes involved. Later, after the collapse of interest in Artificial Intelligence, Hawkins noted, "But the scientific frameworks underlying AI and neural networks were not the right ones to use in building intelligent machines (page 235)." A similar statement applies to understanding actual neural networks.

Zipser et al. chose between static and dynamic memory techniques. They chose the most demanding in electrical power, dynamic memory. Dynamic memory requires continual refreshing of the circuit state to maintain the state. Static memory retains a specific circuit state until some action is taken to change it (if possible). A permanent type static memory is generally described as a write once/ read often memory, or more succinctly a programmable read only memory (PROM). A re-writable PROM is generally described as an electrically programmable read only memory (EPROM). .Since the 1990's, man-made memory devices have essentially abandoned dynamic memory in favor of the more efficient static memory.

Zipser et al. and others have typically employed concepts presently found in "real" as opposed to holonomic, circuit configurations (See **Section 17.1.4.2**). There is a considerable possibility that neural memory circuits employ holonomic techniques to achieve their apparently limitless capacity using a finite substrate. It may be that the technology of man has yet to evolve the type of memory circuit employed in the neural system.

Hawkins proposed an alternate form of memory to that of Zipser et al., based on his explanation of how the

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[45]Hebb, D. (1949) The Organization of Behavior: A Neuropsychological Theory. NY: Wiley

[46]Uttall, W. (2005) Neural Theories of the Mind. Mahwah, NJ: Lawrence Erlbaum Assoc. Section 6.4

[47]Zipser, D. Kehoe, B. Littlewort, G. & Fuster, J. (1993) A Spiking Network Model of Short-Term Active Memory *J Neurosci* vol 13(8), pp 3406-3420

cortex worked, and then noted, “At the same time, I want to stress that this new framework is incomplete (page 108). While presents a variety of conceptual block diagrams, and offers his *memory-prediction framework* of intelligence, his work lacks detail. His analysis does not include any role for the thalamus in vision.

### 17.1.4.3.1 The potential for a delay line form of memory

An observation by this author has always suggested a role for some type of delay line form of memory. He frequently encounters a finite time delay between seeking a piece of information stored in memory and its appearance. It is as if the mind is waiting for the information to circulate along a finite path before reaching the “reading memory station.” This station would essentially be a pattern matching mechanism between what is sought and what is stored.

> In March, 2019, at the age of 83, the re-circulation time of the putative delay line was reduced from about a second or two, to as long as a minute or two. This has made normal speech more difficult, and delayed more technical speech much more difficult.

Fat, like gelatin, could form an extended super crystalline lattice with an extremely low spatial resonance frequency (Section xxx) [xxx not in this chapter ] that would be useful in forming a delay line. The low spatial frequency resonance would be indicative of a low acoustic velocity within the lattice. Such a line could use a conventional neuron as a transducing mechanism and a conventional somasensory (touch) neuron as a reading sensor.

> As a fanciful example; if the long tubular fornix was striated lengthwise, each stria could operate as a separate memory channel, like the tectorial membrane supports a waveguide in the hearing modality. The memory signature of an object could be impressed at one end and read out at the other end. The stria might number in the thousand.

### 17.1.4.4 The formation of memory at the synapse level

Phillips & Pozzo-Miller have recently reviewed their analyses of the relationship between synapses of the central nervous system in establishing memories[48]. Although their motivation related to autism, the material has much broader application. On their page 3, they note, “The plastic nature of dendritic spines and the role of spine morphology in synaptic signaling have led to the hypothesis that dendritic spines are a fundamental component of learning and memory.” They also note, “Though the exact relationship between spine morphology and activity-induced plasticity is still under debate, colloquially the larger, more stable, mushroom and stubby spines are referred to as ‘memory spines’, where as thin spines have been dubbed the ‘learning spines’ for their enhanced ability to undergo structural changes.”
Although potentially significant, reliance on the histology of the spines is not known to be dependable at this time.

While Phillips & Pozzo-Miller rely upon their prior education relative to the chemical nature of the neuron(s), the picture becomes even simpler when explored from the electrolytic theory of the neuron. In fact, a direct analogy can be made between the synaptic connection between two neurons and the early mechanical “cross-bar” switch of telephone switching networks of the 1940's. These switches were replaced by the all-electronic matrix switches of the 1980's and are today replaced by various forms of electronic matrix memories generally known earlier as read-write memories, read only memories or field-programmable memories. Today, they are generally known as programmable gate arrays (PGA).

> PGA’s are widely used in Very Large Scale Integrated circuits (VLSI) that are beginning to approach the circuit density of the biological brain. A more advanced device has recently become popular among engineers. It is a programmable logic array (PLA), a kind of PGA used to implement combinational logic circuits. The PLA has a set of programmable AND gate planes, which link to a set of programmable OR gate planes, which can then be conditionally complemented to produce an output.

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[48]Phillips, M. & Pozzo-Miller, L. (2015) Dendritic spine dysgenesis in Autism Related Disorders *Neurosci Lett*
vol 601, pp 30–40. doi:10.1016/j.neulet.2015.01.011

"The ability of the dendrite to add new spines, change spine morphology, and remove spines in response to synaptic activity has led to the wide-held belief that dendritic spines are the center for synaptic plasticity, and therefore a cellular correlate to learning and memory. In support of this view, many neuropsychiatric disorders, including autism with the high comorbidity of intellectual disability (ID), present with atypical numbers and structure
of dendritic spines, a cellular pathology termed "spine dysgenesis."

While Phillips & Pozzo-Miller describe a variety chemicals generally associated with the synaptic spines of neurons, these are ancillary to the electronic formation of an electronic connection, a synapse, between an axon and a dendrite or podite.

The work of Phillips & Pozzo-Miller will be discussed more extensively in **Section 10.5**. Several papers (27 as of May 2017) have cited Phillips & Pozzo-Miller based on a schlolar.google.com search. Xu, Miller & Pozzo-Miller presented an accompanying cartoon oriented paper based on the accepted wisdom of the chemical neuron[49]. While highly annotated, most of the citations are dated, prior to 2000. Takano, Xu et al. have described neuronal polarization[50]. Their paper is all conceptual and based on caricatures of what they consider the evolution of a neuron based on primarily chemical principles applied to cytology. They do not discuss the source of electrical polarization in the neuron, only that it exists.

This is an exciting new field of research, starting only in 2010, offering exceptionally high dividends following further research. Wang et al. have begun the exploration of pharmacology as a medical treatment for autism and related diseases[51]. Their opening remarks echo, the above remark,

> "Autism spectrum disorders (ASDs) are genetically and clinically heterogeneous and lack effective medications to treat their core symptoms. Studies of syndromic ASDs caused by single gene mutations have provided insights into the pathophysiology of autism. Fragile X and Rett syndromes belong to the syndromic ASDs in which preclinical studies have identified rational targets for drug therapies focused on correcting underlying neural dysfunction. These preclinical discoveries are increasingly translating into exciting human clinical trials. Since there are significant molecular and neurobiological overlaps among ASDs, targeted treatments developed for fragile X and Rett syndromes may be helpful for autism of different etiologies. Here, we review the targeted pharmacological treatment of fragile X and Rett syndromes and discuss related issues in both preclinical studies and clinical trials of potential therapies for the diseases."

## 17.1.4.4.1 The formation of memory at the histological level

The functional formation of a synapse can be described at a more basic level as the formation of an Activa between an axon and a neurite (either dendrite or podite) as illustrated in **Figure 17.1.3-4** In frame B, a high impedance is required in the podite (base lead) if the circuit is to reproduce action potentials. A low impedance can be used for analog signaling as generally used in memory circuits. See **Section 4.2 of PBV**.

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[49]Xu, X. Miller, E. & Pozzo-Miller, L. (2014) Dendritic spine dysgenesis in Rett syndrome *Front. Neuroanat* https://doi.org/10.3389/fnana.2014.00097

[50]Takano, T. Xu, C. Funahashi, Y. et al. (2015) Neuronal polarization *Development* vol 142, pp 2088-2093 doi:10.1242/dev.114454

[51]Wang, H. Pati, S. Pozzo-Miller, L. & Doering, L. (2015) Targeted pharmacological treatment of autism spectrum disorders: fragileX and Rett syndromes *Front Cell Neurosci* doi: 10.3389/fncel.2015.00055

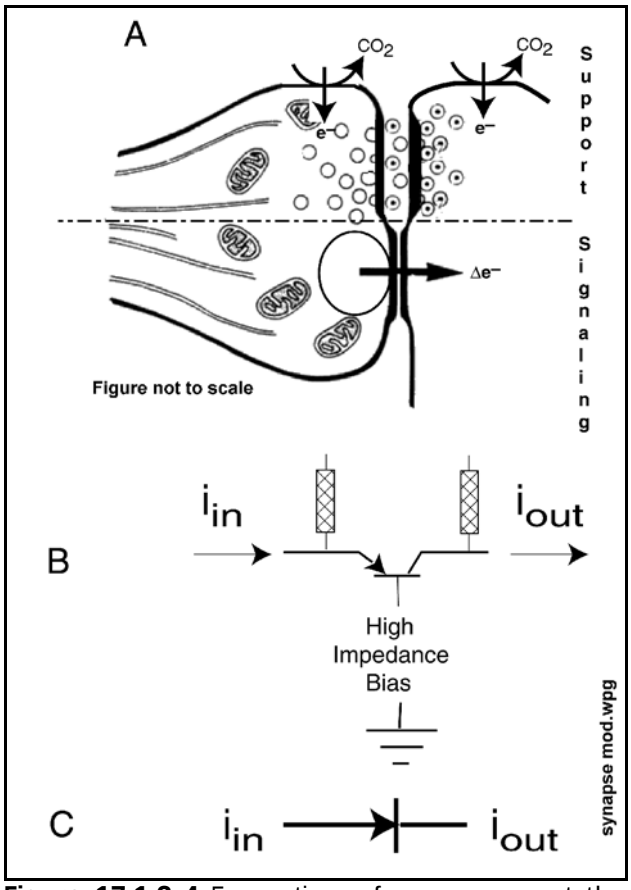


**Figure 17.1.3-4** Formation of a synapse at the cytological, or histological level. A; the symbolic level showing the synapse containing an Activa transfering a signal (horizontal area), two areas of electrostenolytics powering both the axoplasm (left curved arrow) and the neuroplasm of the dendrite or podite (right curved arrow) and various other chemical and cellular materials frequently shown in the literature. B; the equivalent circuit diagram. C; the equivalent circuit element of a synapse when properly biased. See text.

At the electronic topological level, the synapse can be described by **Figure 17.1.3-5**. The key feature of this figure is the distance between the two diodes shown in the upper frame. When these two diodes are brought sufficiently close together, they constitute a single base region shown by the dashed line at lower right. The result is "transistor action" as shown at lower left when properly biased electrically. The critical dimension is a distance between the two base regions of the diodes of less than xxx Angstrom ( xxx nanometers). It is this distance that is achieved when a dendrite and axon come into intimate contact to form a memory unit (with the dendrite feature labeled a memory spine in the nomenclature of Phillips & Pozzo-Miller. Prior to forming such a unit, the dendrite feature is labeled a "learning spine." See Section 4.2.2 of PBV for a broader discussion of this action, or Section 9.4 in "Processes in Biological Vision."

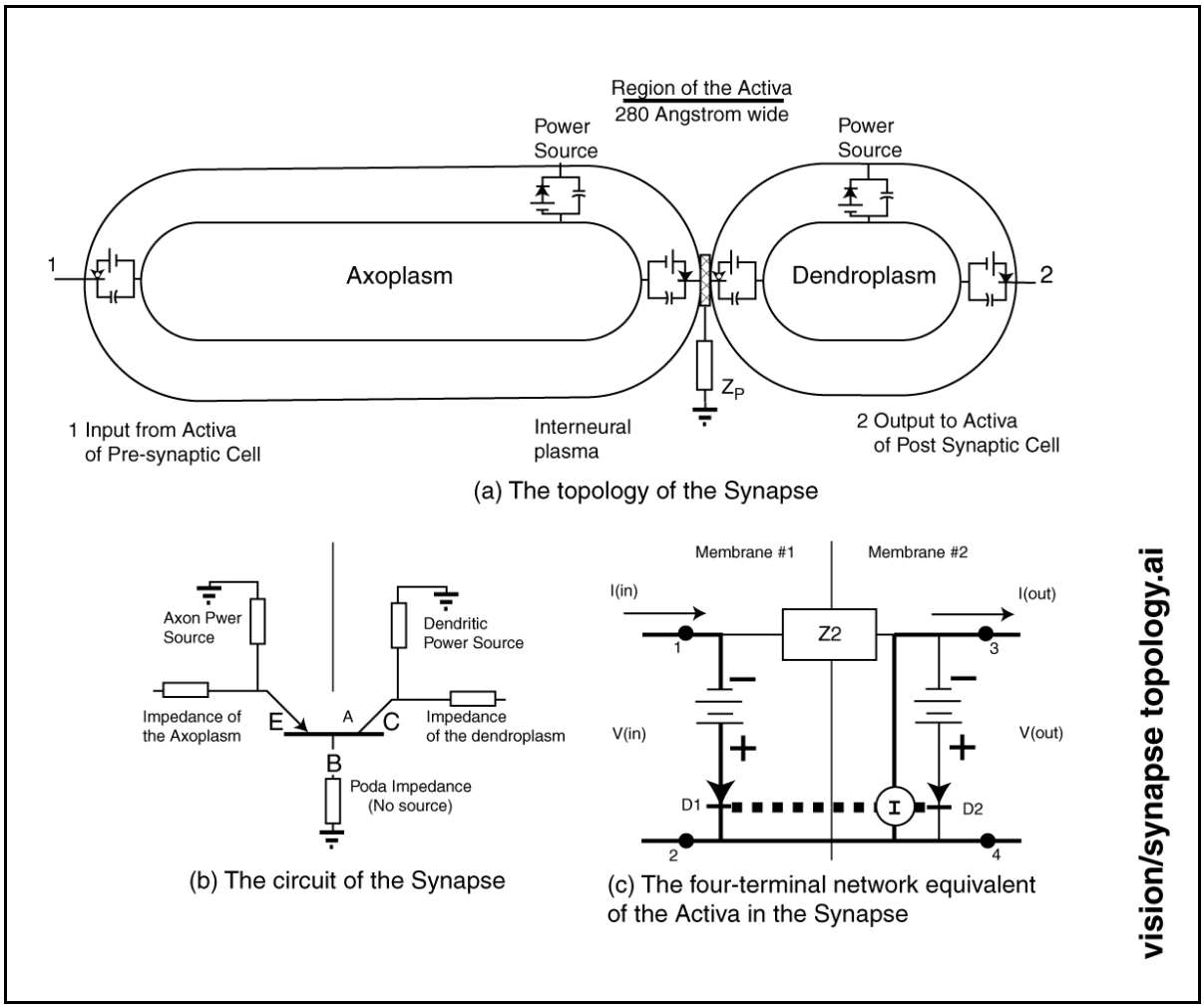


**Figure 17.1.3-5** A mosaic describing a synapse as an Activa, an electrolytic circuit. Upper frame the cytology of a synapse. Lower right frame; the creation of a synapse by bringing two diodes into intimate contact at the base (poditic) terminal level. Lower left frame; the resulting circuit configuration. See text.

At the molecular level, the synapse can be described in considerable detail as in **Figure 17.1.3-6**. It is reproduced from **Section 4.2.2 in PBV** and also in **Section xxx** of this work.

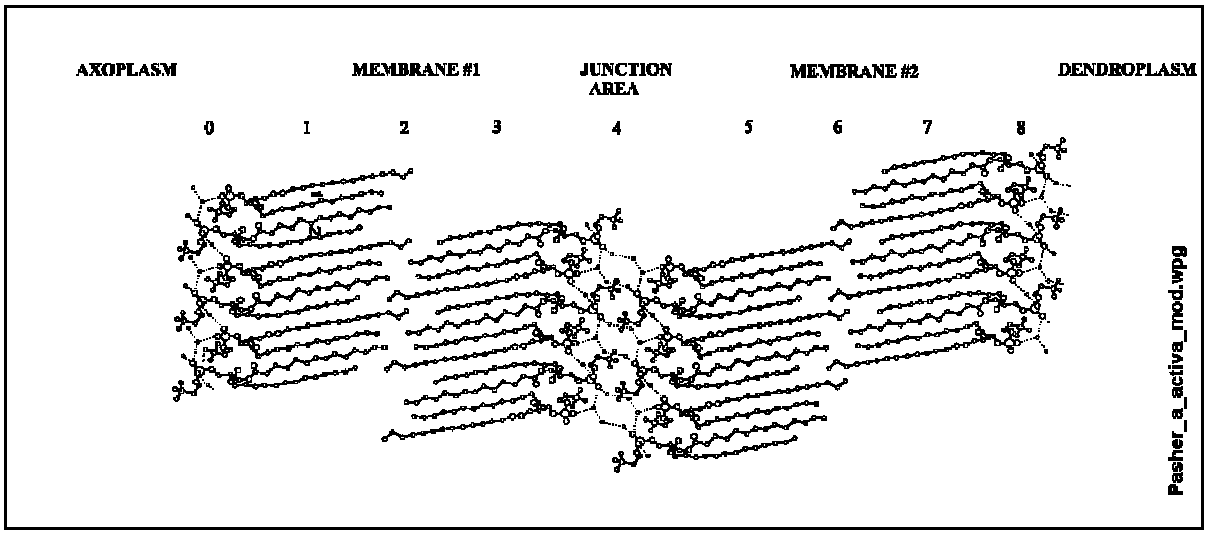


**Figure 17.1.3-6** The synapse at the molecular level. The axoplasm is on the left. The dendroplasm is on the right and the Junction area The development of diffusion tensor imaging (DTI) from the earlier MRI technology has been a boon to the investigators of the cerebellum and its peduncles. It has provided details of this part of the *in-vivo* brain never available before. The result has been an explosion of academic reports in this area during the last ten years. (the base region) is shown in the middle. The membranes are shown as bilayers, each shown as an asymmetrical pair of liquid crystalline leaves exhibiting the electronic characteristics of a diode. The bases of the diodes are separated only by a molecular layer of liquid crystalline water. The water is in contact with the surrounding fluid matrix of the synapse. See text.

## 17.1.5 Forms of cognitive memory

[xxx nottingham lectures until I find Squire material.
[xxx episodic, semantic, mneumonic

Episodic memory is memory related to the spatial and/or temporal characteristics of events.

Semantic memory is memory related to the meaning of things. [xxx nottingham ]

## 17.1.5.xxx Representational memory

Roesch & Schoenbaum have discussed "representational memory" in the context of reward experiments with monkeys[52]. In the context of their discussion (page 207), representational memory is long term memory that represents the external environment, even if it is later found to be incorrect (generally due to trickery by the experimentalist). It may be associated with a judgement as to the utility of the object of attention in that long term memory (such as a food reward).

## 17.1.6 Pseudo memory mechanisms from neurobiology

Several concepts arising from the field of neurobiology, as defined by Rudy, appear quite questionable when examined from the broader purview of neuroscience. At this time, research associated with these concepts is ongoing and seeks to identify their role within the realm of stored memory. With regard to one of these concepts, Rudy noted "To appreciate their discoveries, it is necessary to have a detailed understanding of the methodology used to study LTP and its conceptual basis." This statement appears to also apply to the concept of habituation. Reviewing the databases available and the more modern knowledge now available to neuroscience, these concepts must necessarily be considered pseudo memory mechanisms.

### 17.1.6.1 Habituation, sensitization and dehabituation

During the 2nd half of the 20th Century, and recently reviewed by Rudy in 2008, a *concept* of memory was developed by Kendal, his team and others, in the context of neurobiology (defined in **Section 17.1.1**) augmented by early electrophysiology. Pains were taken to distinguish these mechanisms from the well developed phenomenon of adaptation familiar to scientists working in a variety of sensory modalities. When viewed from the broader purview of neuroscience, instead of neurobiology, habituation, sensitization and dehabituation are clearly phenomena resulting from adaptation within the stage 1 sensory neurons (see **Section 4.12** leading to **Section 2.5.3.5** and other supporting material) and do not involve any distinct memory circuits as defined in this chapter.

### 17.1.6.2 Long Term Potentiation, LTP

A term closely related to habituation is long term potentiation, LTP. This term is also found in the neurobiological category of psychophysics as described in the expanded graphic of Rudy found in **Section 17.1.1** of this work. Rudy discusses the concept on pages 22-26 and associates it with research associated with the hippocampus. From the broader neuroscience perspective, the concept of LTP is highly questionable. Rudy, summarizes the basis for this concept associated with Bliss & Lomo[53] working with rabbits.

#### 17.1.6.2.1 LTP according to Bliss & Lomo

They summarized their results in two areas; Effects of Repetitive Stimulation, Long lasting potentiation.

"Effects of repetitive stimulation

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[52]Roesch, M. & Schoenbaum, G. (2006) From associations to expectancies: orbitofrontal cortex as gateway between the limbic system and representational memory *In* Zald, D. & Rauch, S. *eds*. The Orbitofrontal Cortex. Oxford: Oxford Univ Press. Chapter 8

[53]Bliss, T. & Lomo, T. (1973) Long-lasting Potentiation of Synaptic Transmission in the Dentate Area of the Anaesthetized Rabbit following Stimulation of the Perforant Path *J Physiol* vol 232, pp 331-356

Stimulation of the perforant path at 10-15/sec for several seconds normally resulted in the following sequence of events.

1. A rapid build-up of the population spike during the conditioning train.
2. A brief (1-2 sec) period of spike potentiation immediately after the conditioning train.
3. A phase of spike depression lasting from a few seconds to more than a minute.
4. A phase of potentiation, sometimes lasting for several hours, and in many cases involving synaptic as well as spike components of the response.

Although there was considerable variation in the degree and duration of these four phases in different preparations, the sequence as a whole was a characteristic feature of the experiments." This last sentence characterizes the experimental precision achievable in the field of neurobiology and electrophysiology during the third quarter of the 20th Century. In the above quotation, it appears the term synaptic refers to an analog generator potential whereas the term spike implies a pulse(s) associated with action potentials. Their figure 2, obtained by recording galvanometer readings on film, are difficult to interpret compared to modern instrumentation. The waveforms appear to represent the stimulation of a stage xxx neuron by a series of low level and narrow pulses relative to the time constants of the stimulated neuron. The "population evoked presynaptic potential (e.p.s.p.)" shows an undershoot followed by an overshoot (the maintained potentiation) sustained in attempting to return to the baseline in the presence of sustained low-level stimulation. ***This maintained potentiation may result from the integration of the continuing low level stimulation.***

"*Long lasting potentiation*

The potentiation which followed a conditioning train varied considerably in both duration and degree from experiment to experiment. If long-lasting potentiation is arbitrarily defined as potentiation lasting 30 min or more, then a positive result was obtained in fifteen out of eighteen animals. In most animals more than one pathway was conditioned. A total of twenty-four out of the thirty-five conditioned pathways showed long-lasting potentiation. Potentiation of all three parameters was observed in nine of the thirty-five conditioned pathways, although in some cases more than one conditioning train was needed to achieve this result. Considering the response parameters separately, a decrease in spike latency was the commonest form of facilitation (twenty pathways). The population e.p.s.p. was potentiated in fifteen pathways and the spike in fourteen pathways. A lack of correlation between e.p.s.p. and spike potentiation was a notable feature of several experiments . . ." They provide considerable more discussion, but the limited capability of their instrumentation at that time stands out. Their demonstration of long term potentiation as a unique mechanism, separate from adaptation in the stage 1 sensory neuron(s) and the continuing low level stimulation used in their protocol, appears highly questionable.

Bliss & Lomo conclude their paper with an interesting remark, "Whether or not the intact animal makes use in real life of a property which has been revealed by synchronous, repetitive volleys to a population of fibres the normal rate and pattern of activity along which are unknown, is another matter." Repeating their experiments using a more realistic protocol and better knowledge of the fundamental circuits involved is required to justify considering long term potentiation as more than a concept.

## 17.2 Declaratory memory

Declaratory memory is a term popularized by Squire in his broadly disseminated lectures of xxx. [xxx add ] The working definition dates from Milner, Squire & Kandel of 1998, "Declarative memory is associated with "knowing that" (the knowledge of abstract facts and events) as opposed to nondeclarative memory, the memory involved in "knowing how" (as in the knowledge of motor skills)." See **Section 17.1.2** and **Section 17.1.3**.

### 17.2.1 Memory and the prefrontal lobe

Wagner et al. have provided very provocative discussion of the association of the prefrontal cortex with

episodic memory[54]. Their material is reviewed in Section 12.xxx.

It is believed that most episodic memory is stored as long term memory with the aid of the hippocampus. Recent fMRI studies have begun to localize the part of the hippocampus associated with memory[55]. "fMRI studies have often demonstrated that much of the activation is located more posteriorly in the parahippocampal formation, at least for visual stimuli."

Wolters & Raffone have presented a quite different view concerning the role of a "central executive" that sounds like the conscious executive of this work[56]. However, they conceptually embed their central executive within their working memory (that sounds a lot like the declaratory memory of this work). Their discussion is largely conceptual with many caveats associated with their one block diagram of the engines of the prefrontal lobe.

## 17.2.2 Memory, the basal ganglia and hippocampus

[xxx review 4th ed of Fuster and the material in 17.1.2 and 12.5.4 ]

> Most of the signaling paths associated with the limbic system, the fornix and the hippocampal formation have been deduced from traffic analysis. Establishing the signal paths by traffic analysis between pairs of points operating sequentially is fairly routine and successful. When more than four points and simultaneous signaling is involved, the task is much more difficult and ambiguous. Figures in the literature describing signal paths between multiple points frequently differ significantly between investigators. Many nodes are omitted from one diagram and many other nodes are included. In all cases, the points enumerated are more likely to be mediating points along a much more complex path and not specific nodes.

**Figure 17.2.2-1** is reproduced from Squire & Dede in Kandel et al., 2016[57]. The paper provides a clear description of the nature of and many engines associated with declarative memory. However, many of the signaling paths shown are reinterant. The bottom box illustrates the complex intercommunications of the basal ganglia and the other lobes of the CNS. The text includes additional relationships with other engines. These relationships appear to be based primarily on traffic analysis, mainly on neuron counts between two points. The elements within the hippocampus were not clearly defined, although they undoubtedly are in the many accompanying citations. See **Section 10.2.5**.

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[54]Wagner, A. Desmond, J. Glover, G. & Gabrieli, J. (1998) Prefrontal cortex and recognition: Functional MRI evidence for context-dependent retrieval processes Brain vol 121, pp 1985-2002

[55]Binder, J. & Detre, J. (2005) Functional MRI in elipepsy *In* Kuzniescky, R. & Jackson, G. *eds*. Magnetic Resonance in Epilepsy. NY: Elsevier Chap 10

[56]Wolters, G. & Raffone, A. (2008) Coherence and recurrency: maintenance, control and integration in working memory *Cogn Process* vol 9, pp 1-17

[57]Squire, L. & Dede, A. (2016) Conscious and Unconscious memory systems *in* Kandel, E. Dudai, Y. & Mayford, M. *eds.* Learning and Memory. NY: Cold Spring Harbor Laboratory Press pg 4

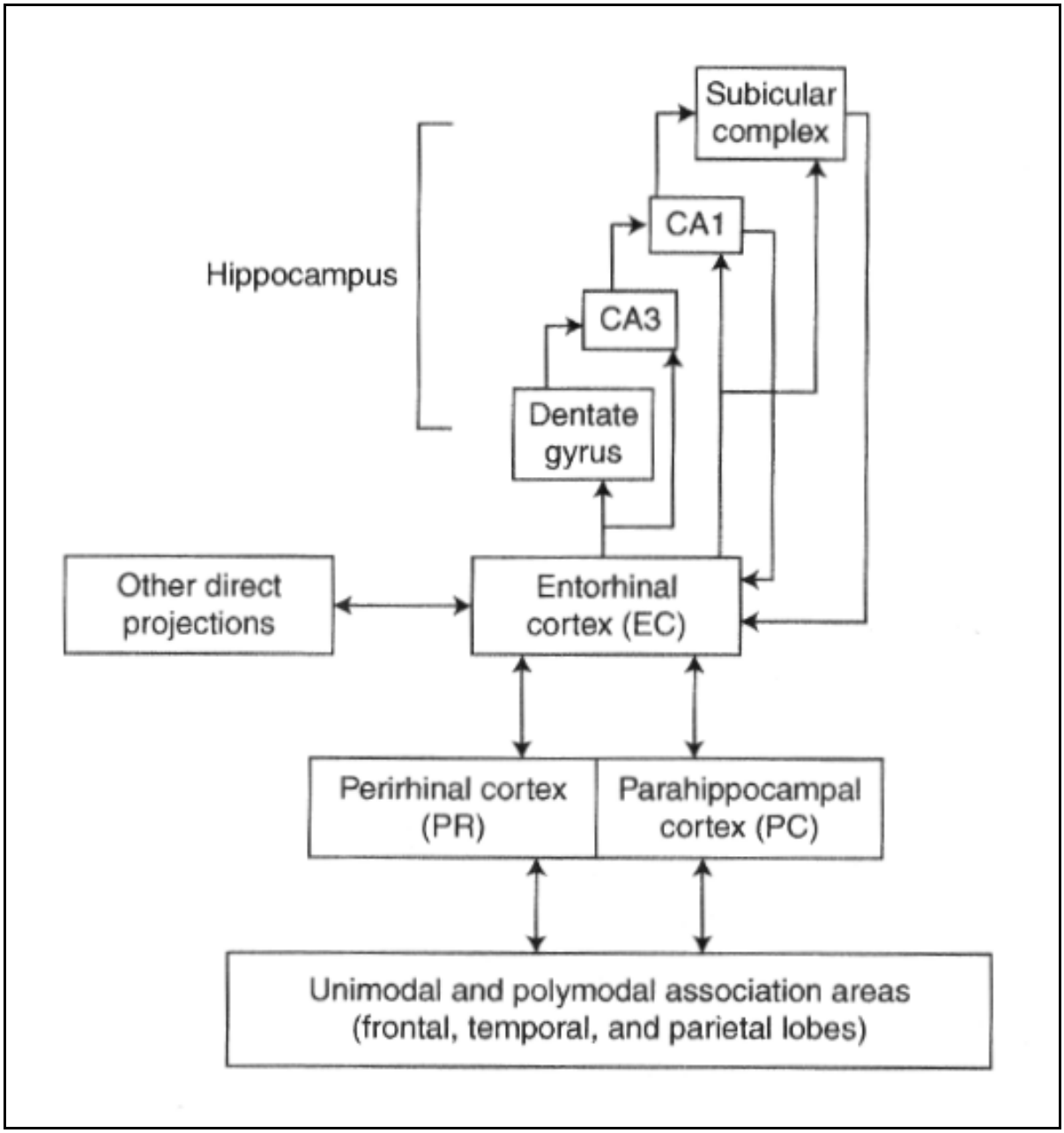


**Figure 17.2.2-1** Schematic of the medial temporal lobe memory system for declarative memory, which includes the hippocampus and other designated engines. The schematic is described as hierarchical by the authors. CA1 & CA3 were not further defined in the Squire & Dede paper. See text. From Squire & Dede, 2016

They also note important connections between the illustrated engines and those of the diencephalon, including the anterior thalamic nuclei and the mammillothalamic tract, related to declarative memory. They note, "Damage to these structures causes the same core deficit as damage to the medial temporal lobe, probably because these nuclei and tracts are anatomically related to the medial temporal lobe." This work asserts an even stronger functional connection between the thalamic engines and tracts and the medial temporal lobe.[xxx add from paper after further study ]

The conclusion section is very concise and useful. As stressed in this work, they assert, "The memory system framework is fundamental to the contemporary study of learning and memory." While they stress the anatomical relationships between engines and larger entities, it is the functional relationships between various individual engines that is of critical importance. They note after discussion of a variety of situations, "the therapeutic targets for various kinds of memory disorders are quite different" followed by several examples.

## 17.2.2.1 Major neural circuit paths supporting the hippocampus

> Both the hippocampus and the cerebellum support major peduncles between them. However, since these connections are neither visible from lateral or medial projected images of the brain, their importance is generally overlooked. Only sagittal views of the brain illustrate these pedunclear connections adequately. It should be noted that many illustrations of the brain show the cerebellum cut away for greater clarity of other features. This is unfortunate. Most recent calculations show the cerebellum contains 75% or more of all of the neurons in the CNS.
>
> Herculano-Houzel[58], provided a new appreciation of the importance of the cerebellum;
>
> "It turns out that the human brain has on average 86 billion neurons, with 69 billion of them located in the cerebellum. The entire cortex, the area that we think is responsible for human thought and culture, has only 17 billion (19% of all the neutron in the brain and similar to the percent found in other mammals), leaving only one billion for the entire rest of the brain. Not only that, but the visual and other sensory areas and the motor cortex have way more neurons that the frontal lobes (including the prefrontal cortex—that part of the human brain that is involved with all the high end abilities such as memory and planning, cognitive flexibility, abstract thinking, initiating appropriate behavior and inhibiting inappropriate behavior, learning rules and picking out relevant information perceived through the senses)."

Duvernoy (2005) discusses the role of the hippocampus in memory in his section 3.3 without developing the details. His comments appear to be based totally on traffic analysis (interconnection of neurons and possibly fascicles, consisting of multiple neurons, without knowledge of the messages carried). On his page 257, Rudy (2008) makes the bold statement in a section title that "The Hippocampus Does Not Store Content." This is a strange position to take since he offered no support for this assertion. Nine years later there remains no evidence of how or what constitutes a memory storage site, or where it might be located.

> *The developing hypothesis of hippocampus operation, in this work, is that the hippocampus can store short term memories (measured in seconds to minutes)supporting stage 5, and is part of the path leading to long term storage and recall of memories within the cerebellum.*

Rudy reviews the widely held view known as the Indexing Theory of Episodic Memory. The discussion is clearly conceptual. The concept is that any stage 4 engine in the CNS that extracts a piece of episodic information, establishes a "memory trace" by "activating patterns of neocortical activity, which then project to the hippocampus. As a consequence, synapses in the hippocampus responding to the neocortical inputs are strengthened." Note the concept does not suggest any new synapses are formed, only existing synapses are strengthened in some non–described manner.

Duvernoy begins the section with the disclaimer, "This section goes beyond the author's field of research, is based on an abundant body of work found in the literature (with citations)." He also notes, " It should be noted that some of the results presented here are controversial and may thus be subject to discussion." This author would take exception with Duvernoy with regard to the age and the depth of the reported research, particularly at the histological level and the functional (operational) level.

Duvernoy begins his section by noting, "The possible (operational) functions of the hippocampus are divided into four categories:

1. Learning and memory,

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[58]Herculano-Houzel, S. (2009) The human brain in numbers: a linearly scaled-up primate brain *Front Human Neurosci* vol 3, art 31 doi: 10.3389/neuro.09.031.2009

2. Regulation of emotional behavior,
3. Certain aspects of motor control, and
4. Regulation of hypothalamic functions.

Only the first of these categories is of interest in this section.

Duvernoy noted, "It is generally admitted that the hippocampus has a critical role in learning and memory. Information arising from large isocortical zones converges to the entorhinal area and then to the hippocampus. Thus newly acquired items cross the hippocampal filter before being fixed in the isocortex."

The definition of terms is in a poor condition in this area. Merriam-Webster's On-line Medical Dictionary provides the following, less than adequate (overlapping) definitions,

> **Isocortex**–The larger part of the cerebral cortex, that is distinguished from the allocortex by having a larger number of nerve cells arranged in six layers. Also called homotypic cortex , neocortex , neopallium .
> **Allocortex** (**archipallium**)--the olfactory part of the cerebral cortex comprising the hippocampus and part of the parahippocampal gyrus
> **Neopallium**– the phylogenetically new part of the cerebral cortex that develops from the area between the piriform lobe and the hippocampus, comprises the nonolfactory region of the cortex, and attains its maximum development in humans where it makes up the greater part of the cerebral hemisphere on each side –called also isocortex.

Duvernoy did highlight two major neural pathways involving the hippocampus; "the *polysynaptic pathway*, which links all parts of the hippocampus by a long neuronal chain, and the *direct pathway*, which directly reaches the output neurons of the hippocampus."

Squire & Dede provided a wide range of definitions from their perspective. Appropriately, the definitions are becoming longer to adequately define their scope.

**Declarative memory–** has two major components; semantic memory(facts about the world) and episodic memory (the ability to re-expereince a time-and-place-specific in its original context (Tulving, 1983).

**Non-declarative memory–** is an umbrella term referring to multiple forms of memory that are not declarative. It is typically dispositional and is expressed through performance rather than recollection. It supports myriad ways of responding to the world.

## 17.2.2.1.1 The polysynaptic pathway

The intrahippocampal circuitry of the polysynaptic pathway "is composed of a long neuronal chain, made up of the entorhinal area, the gyrus dentatus, CA3, CA1 and the subiculum. "The polysynaptic pathway originates in layer II of the entorhinal cortex."

"The CA2 field, which has not yet been discussed here but is in fact quite distinct in humans, has an obscure role. Its marked cellular density and its intense vasculaization might, however correspond to a particular function." This comment could hardly be less informative.

"Since Ramon y Cajal's description, axons of CA1 have been considered the main output of the hippocampus by way of the alveus and then the fimbria. Currently, a supplementary link is considered to be joined to the chain, a link formed by the subiculum. Thus, by entering the alveus, the axons of CA1 produce collaterals which reach the subiculum

The subiculum therefore emits the definitive response, by fibers constituting the major part of the alveus and then the fimbria." This traffic analysis is at a more detailed level than that of Duvernoy in **Section 10.2.5**. However, it is still devoid of any clues to the character of the signals projected.

## 17.2.2.1.2 The direct pathway

- - - -

**Figure 17.2.2-2** shows the principle afferent and efferent connections of the hippocampal formation.

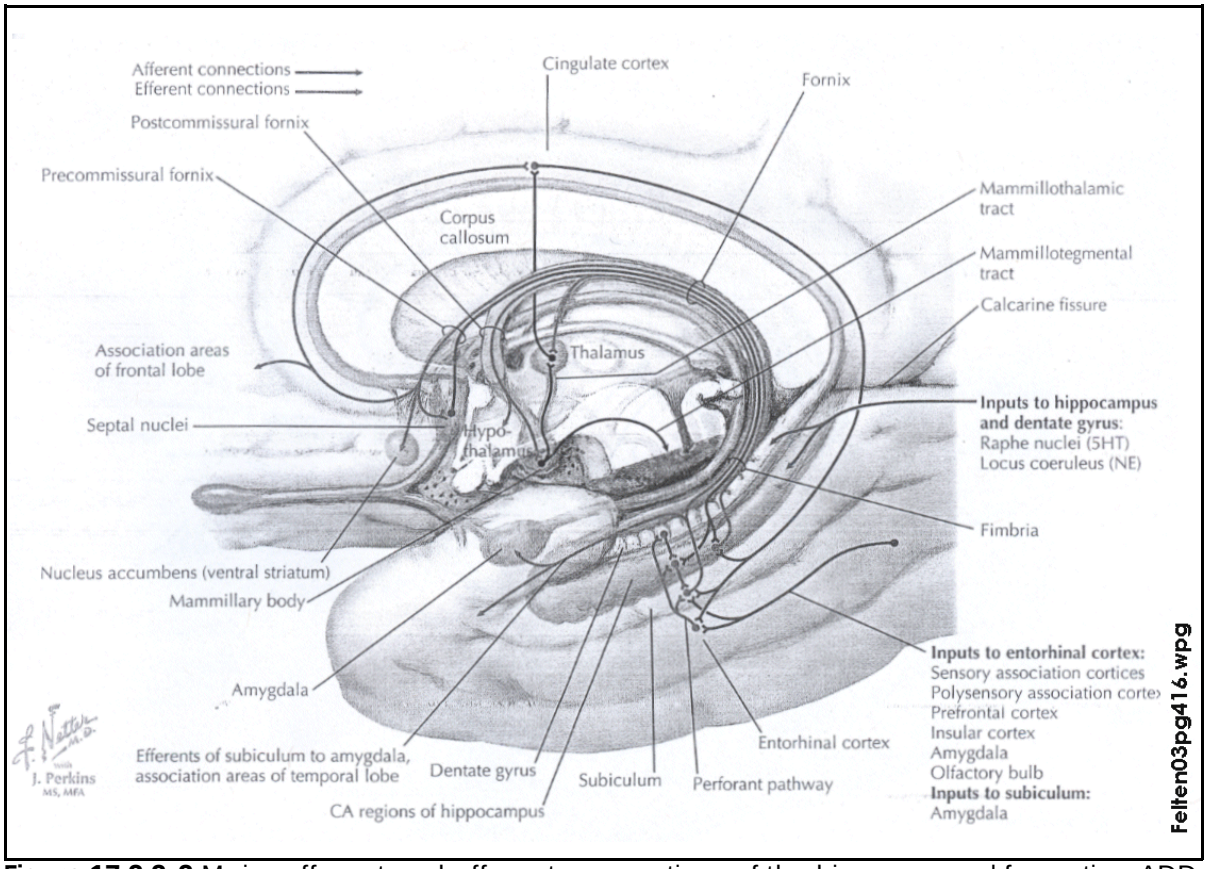


**Figure 17.2.2-2** Major afferent and efferent connections of the hippocampal formation ADD. See text. From Felten & Shetty, 2003.

## 17.2.2.1.3 More detailed connections to the hippocampus

**Figure 17.2.2-3** shows a coarse schematic of the hippocampus overlaid on a cytoarchitectural map.

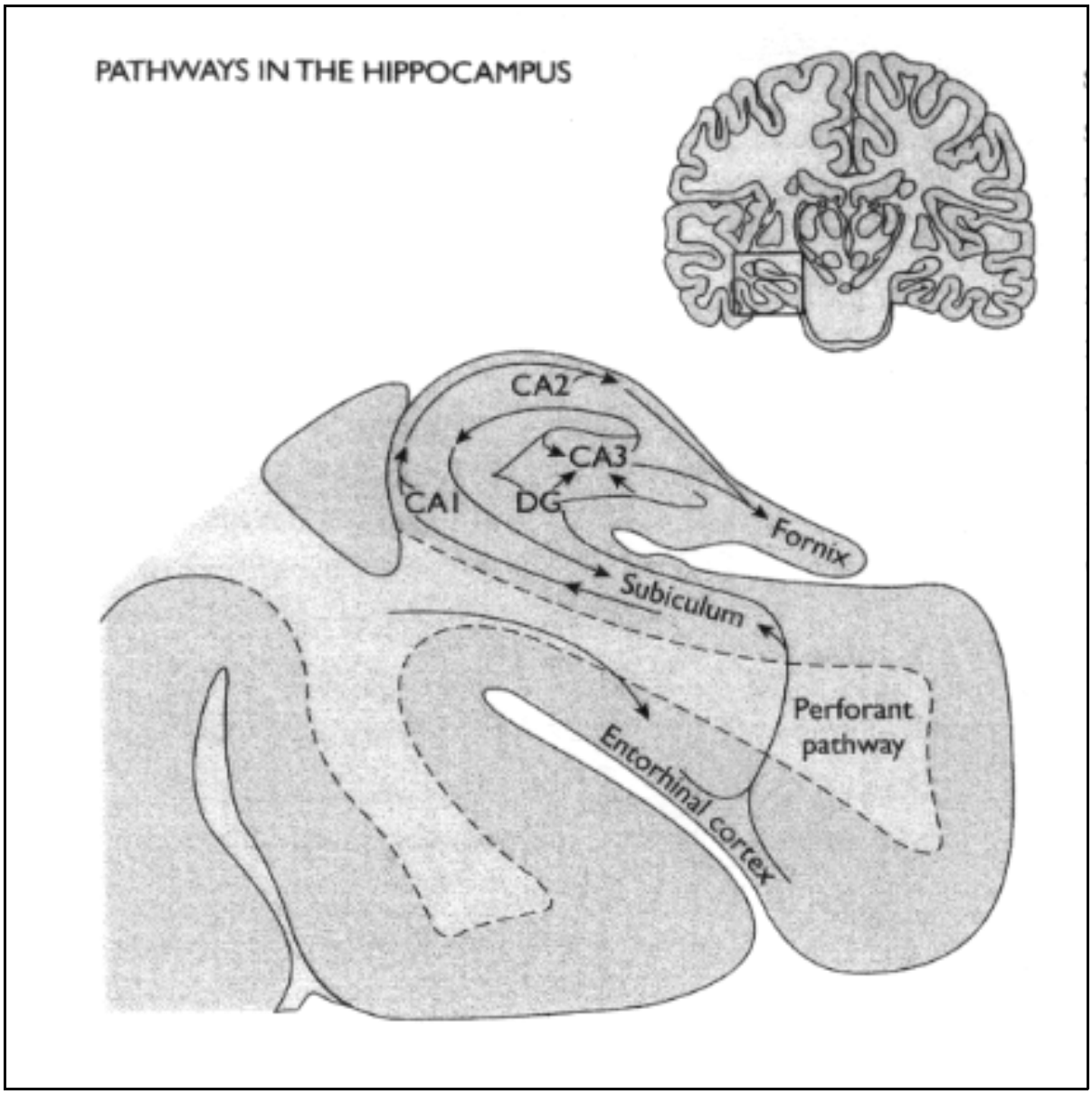


**Figure 17.2.2-3** Partial schematic overlaid on the cytoarchitecture of the hippocampus ADD. Inset at upper right shows the location of the composite image in the lower left. The paths are not comprehensive and do not form a contiguous schematic. See text. From Squire & Kandel, 2009.

**Figure 17.2.2-4** shows a slightly more detailed view indicating areas CA1, CA2 & CA3 of the hippocampus. Only two of the CA designated areas include any distinct input or output. CA2 does not. The pyramid neuron symbols used can be expected to represent stage 3 signal projection neurons of the stage 3B type when receiving signals at their dendritic terminal, decoding pulse streams from other engines of the CNS. When sending signals to other engines, they can be considered stage 3A type encoding analog information into a

pulse stream. Note the group of neurons exiting at the top of the figure without any clear destination, except to label the group as "Alveus." The list of potential input signals at lower right is less than specific.

In a previous figure not reproduced here, Felten & Shetty note, "The hippocampal formation consists of the dentate gyrus, the hippocampus proper (cornu ammonis [CA] regions), and the subcilium These structures are intimately interconnected with the adjacent entorhinal cortex. . . .The hippocampus is divided into several zones of pyramidal cells, called CA regions (CA1–CA4). This is the only reference to CA4 in Felten & Shetty, and the first time this analyst has encountered it in the literature. The dentate gyrus and hippocampus are three–layered cortical structures. Granule cells populate the dentate gyrus, and pyramidal cells are the main neurons in the CA region of the hippocampus. The hippocampal formation has extensive interconnections with cortical association area and with limbic forebrain structures, such as the septal nuclei and the cingulate gyrus." It is not clear whether they are speaking about a large population of pyramidal cells, or primarily the larger, or smaller, pyramidal cells. The larger ones typically represent stage 3 neurons. The smaller ones may be present in profusion, some of which may be too small to identify with light microscopy. Felten & Shetty also note, "Pyramidal cells in the CA1 region of the hippocampus are particularly vulnerable to apoptosis resulting from ischemia." and "CA3 pyramidal neurons are particularly vulnerable to high or persistently elevated levels of cortisol (or synthetic glucocorticoids), resulting in similar functional deficits." They describe the clinical situation related to these conditions in some detail.

In the anatomical notes accompanying this figure, Felten & Shetty note,

> "The hippocampal formation has an internal circuitry that is interconnected with the entorhinal cortex. Pyramidal neurons of the entorhinal cortex send axons to granule cell dendrites in the dentate gyrus. These granule cell axons (mossy fibers) synapse on pyramidal cell dendrites in CA3. Pyramidal cells in CA3 project to pyramidal cell dendrites in CA1 (Schaffer collaterals) and CA2. Ca1 pyramidal axons project to pyramidal neurons in the subiculum. The subiculum sends axonal projections back to the pyramidal neurons of the entorhinal cortex. This information flow represents an internal circuit. Superimposed on this circuitry is a host of interconnections with association regions of the neocortex and other limbic forebrain structures. Neurons of the subiculum and pyramidal neurons of CA1 and CA3 send axons into the fornix as efferent projections to target structures. The subiculum also sends axons to the amygdala and association area of the temporal lobe."

By re-annotating the above material using the terminology of this work, a clearer, and yet briefer text can be provided. All of the pyramidal cells described here should be labeled stage 3 signal projection neurons. Those sending signals to a different engines should be labeled stage 3A analog signal encoding neurons and all of those receiving signals at their dendrites (or in fact their podites) should be labeled stage 3B pulse decoding neurons that regenerate the encoded analog signal(s). The granule cells of this discussion can be assumed to be stage 4 analog information extraction neurons. The granule cells, if examined down to sub-micron dimensions, will outnumber the pyramid cells by at least 1000:1. The Schaffer collaterals, as described, are clearly axons of stage 3A pyramidal encoding neurons.

Three more definitions are needed at this point;

**Schaffer collaterals–** axon collaterals unique to the hippocampal formation.

**Mossy fibers–** axons of granule cells typically associated with the cerebellum. [xxx ]

**Climbing fibers–** axons of xxx neurons typically associated with the cerebellum. [xxx ]

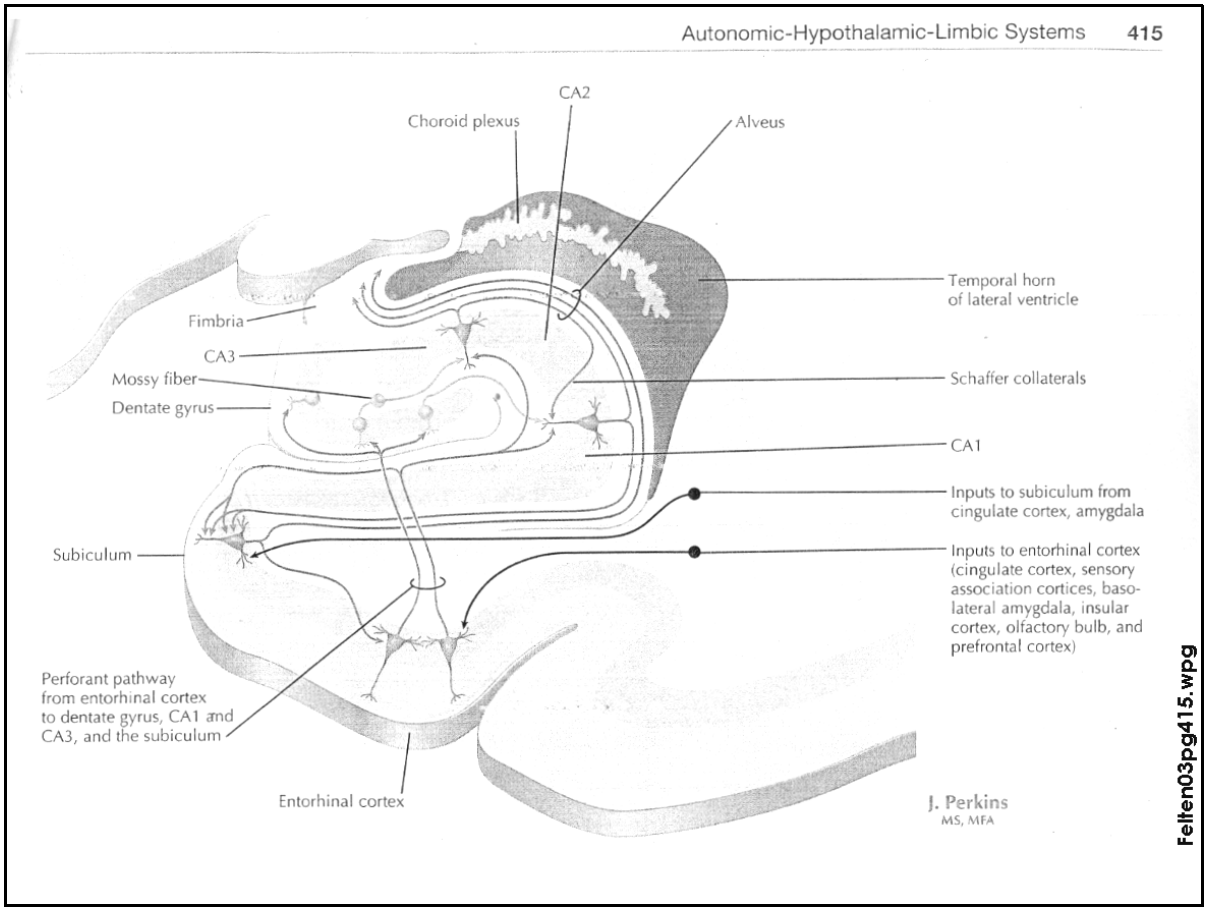


**Figure 17.2.2-4** More detailed connections to CA1, CA2 & CA3 of the hippocampus. The long list of sources at lower right constitutes a "shopping list" rather than adequate scientific knowledge. See text. From Felten & Shetty, 2003.

## 17.2.2.1.4 Clinical notes on the relationship– hippocampus & Alzheimer's.

In the clinical notes to the detailed connections figure, Felten & Shetty assert,

> "Many of these cortical regions ar particularly susceptible to neuronal degeneration in Alzheimer's disease (AD), a neurodegenerative disease that damages and destroys neurons in the cerebral cortex and higher centers of the brain, and is accompanied by market cognitive deficits. Disruption of hippocampal circuitry leads to the inability to consolidate immediate and short-term memory into long-term traces. Temporal lobe damage and disruption of connections with the basal forebrain, cingulae cortex, frontal cortex, and other forebrain structures also affected by AD contribute to the marked cognitive decline in patients with AD. In AD, the brain shows extensive neuronal loss, impaired functioning of synaptic connections, and damage to important neurotransmitter systems that participate in functions such as memory. AD is characterized by the accumulation of altered and aberrant proteins inside neurons, called neurofibrillary tangles, and outside of neurons, called senile plaqures. However, severe cognitive decline may occur in the absence of neurofibrillary tangles and senile plaques, and the presence of these proteins in the brain is not always predictive of cognitive dysfunction. Proposed causes of AD include the accumulation of beta-amyloid protein and its precursor protein and/or excessive phosphorylation of an important protein (tau) that helps to give neurons their structural integrity. A form of apolipoprotein E (epsilon 4) is linked with excessive production of free radicals

that may kill neurons. Inflammatory molecules (e.g., 1L-1beta) also may cause neuronal damage. ***At present, there is no common agreement on a specific sequence of events or cascade of pathology in AD***." [emphasis added]

Ingram has presented a popular book describing the above terms in more precise but still common language[59]. His focus was on Alzheimer's Disease, its history, current understanding of its cause and progression, and the potential for a cure during the next few decades.

Both of these papers will be addressed in **Section 15.4.3**.

### 17.2.2.2 Place cells in the hippocampus

Moser, Rowland & Moser have provided a paper illustrating new functional relationships within the hippocampus[60]. Their aim "is to show how studies of hippocampal neuronal activity during the past few decades have brought us to a point at which a mechanistic basis of memory formation is beginning to surface." Unfortunately, their work still relies upon the firing of stage 3 signal encoding and propagation cells. But the paper offers an important step. Their two-dimensional graphics suggests the action potential generating neurons are on the surface of an engine.

## 17.2.3 The amygdalae in the Limbic System

Siebert et al[61]. discusses the *bilateral symmetry of the limbic system, including the pair of amygdala*. This symmetry is usually not considered in most papers.

Rudy (2008) offered only two short discussions related to the amygdala. On page 199, he discusses "the Great Modulator: the Amygdala." A block diagram is provided with the amygdala at the center and many output paths but no input path to it. The text aims to establish that the amygdala plays an important role in establishing memories. After illustrating both the place-learning and visible-platform versions of the Morris water-escape task, he asserts, "Thus the amygdala is not a critical storage site for these memories. Instead, the hippocampus is a key storage area for the place-learning memory, and the caudate is thought to be important for the acquisition and storage of the memory for the visible-platform task."

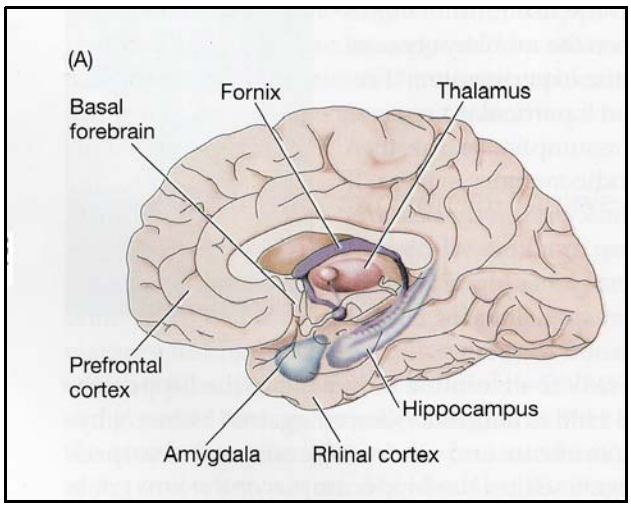


**Figure 17.2.3-1** Sagittal view of the human brain, emphasizing the amygdala. From Rudy, after Murray & Mishkin, 1998.

**Figure 17.2.3-2** reproduced from figure 12.5 in Rudy, shows the amydala in relation to other nearby elements with an interesting assertion in the original caption attributed to Squire, 1987,

"Primates with damage to both the amygdala

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[59]Ingram, J. (2016) The End of Memory. NY: St. Martin's Press

[60]Moser, M-B. Rowland, D. & Moser, E. (2016) Place cells, grid cells, and memory *in* Kandel, E. Dudai, Y. & Mayford, M. *eds.* Learning and Memory. NY: Cold Spring Harbor Laboratory Press pp 289-303

[61]Siebert, M. Markowitsch, H. & Bartel, P. (2003) Amygdala, affect and cognition: evidence from 10 patients with Urbach-Wiethe disease *Brain* vol 126, pp 2627-2637 DOI: 10.1093/brain/awg271

and hippocampus (AH) performed normally. However, removal of the rhinal cortical regions profoundly disrupted performance" on the delayed nonmatching to sample, DNMS, task.

He makes the optimistic statement on page 207, "Researchers now have a good understanding of the primary factors involved in initiating amygdala–dependent memory modulation." After only a few remarks, he then notes, "Unfortunately, at this time very little is known about what happens when inputs from the amygdala arrive at storage circuits." There is no discussion of the character of the input and/or output signals. His block diagram on page 273 does not include the amygdala in any control function.

The amygdala is generally associated with the "fight or flight" reflex.

### 17.2.3.1 Connections of the amygdala within the Limbic System

Felten & Shetty have reproduced many of the figures originally prepared by Netter. A majority of them are suitable for pedagogy but are now outdated for use in actual surgery. The figures show primarily arrows pointing to various other structures and the tabulation on page 419 is primarily conceptual and does not show any input specifically from, or to, the primary memory.

**Figure 17.2.3-2** shows the major afferent connections to the amygdala.

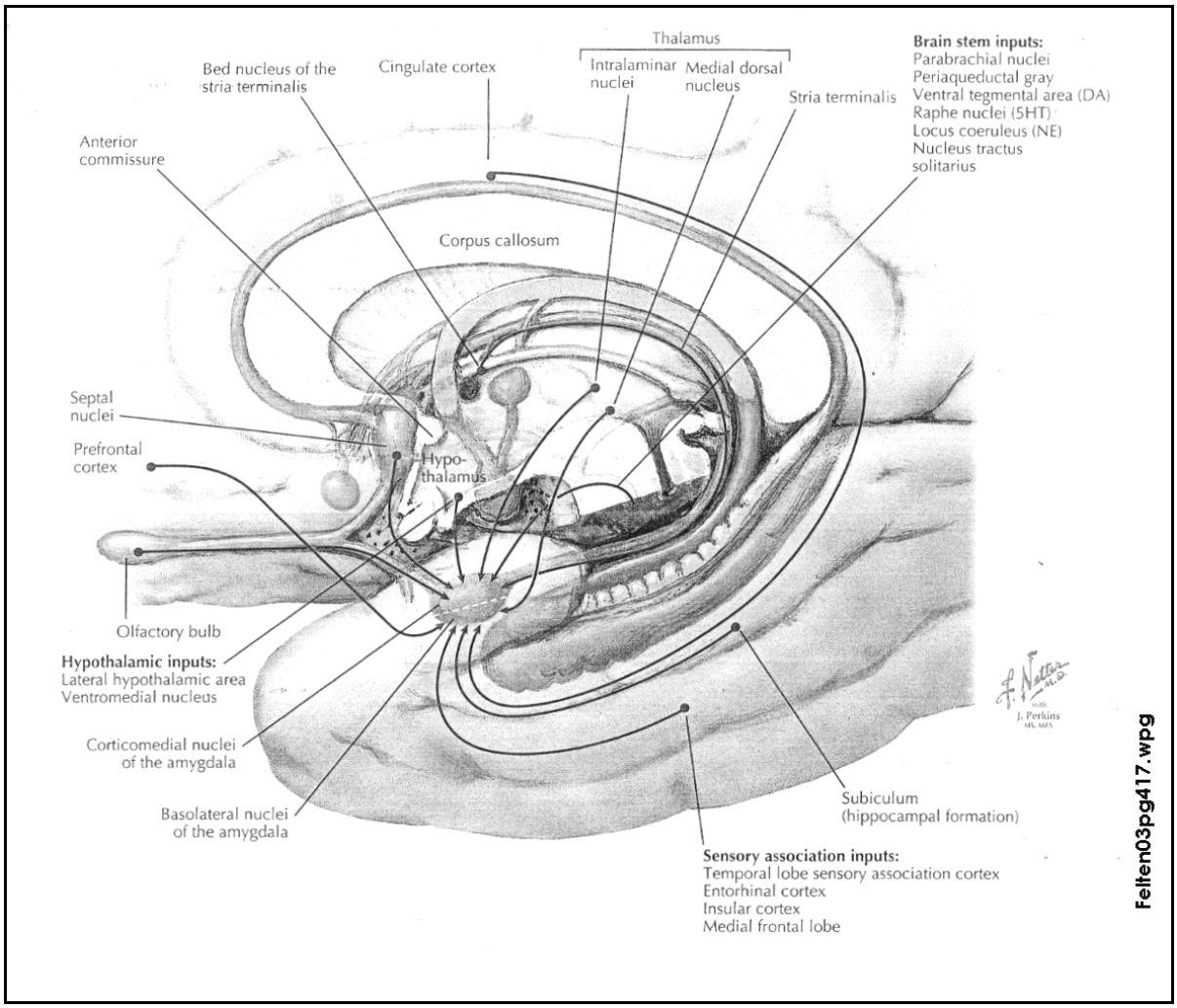


**Figure 17.2.3-2** Major afferent connections of the amygdala ADD. Note the digitationes along the dentate gyrus, and the less obvious and wider spaced digitationes along the lower surface of the hippocampus below the dentate gyrus. See text. From Felten & Shetty, 2003.

**Figure 17.2.3-3** shows the major efferent connections to the amygdala.

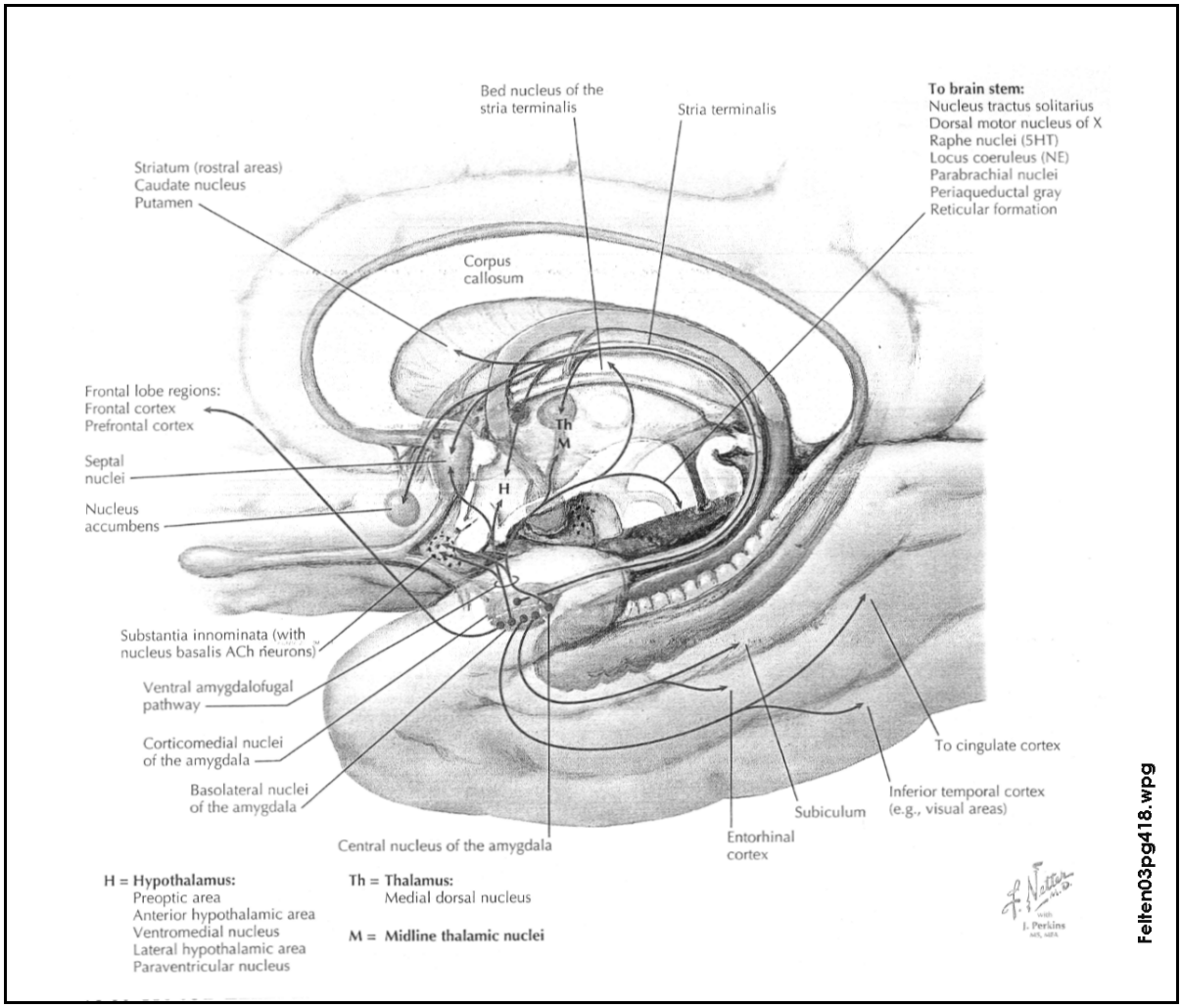


**Figure 17.2.3-3** Major efferent connections of the amygdala ADD From Felten & Shetty, 2003

**Figure 17.2.3-4**

## 17.2.3.1 Connections of the amygdala within the Limbic System

## 17.2.4 Connections involving the Septal Nuclei

A brief search of the internet citing the septal nucleus results in significant conflicts of opinion. Wikipedia (fall 2017) notes,

> "The septal nuclei (medial olfactory area) are a set of structures that lie below the rostrum of the corpus callosum, anterior to the lamina terminalis (the layer of gray matter in the brain connecting the optic chiasma and the anterior commissure where the latter becomes continuous with the rostral lamina). The septal nuclei are composed of medium-size neurons which are classified into medial, lateral, and posterior groups. The septal nuclei receive reciprocal connections from the olfactory bulb, hippocampus, amygdala, hypothalamus, midbrain, habenula, cingulate gyrus, and thalamus. The septal area (medial olfactory area) has no relation to the sense of smell, but it is considered a pleasure zone in animals. The septal nuclei play a role in reward and reinforcement along with the nucleus accumbens. In the 1950s, Olds & Milner showed that rats with electrodes implanted in this area will self-stimulate repeatedly (i.e. press a bar to receive electrical current that will stimulate the neurons). Experiments on the septal area of man have taken place since the 1960s."

Under the title, "Connections with other structures" it goes on,

> "The dorsal septum projects to the lateral preoptic area, lateral hypothalamus, periventricular hypothalamus and midline thalamus.
>
> Fibers from the ventral half of the septum project topographically to the hippocampal formation, thalamus, hypothalamus and midbrain. Specifically, neurons located along the midline in the vertical limb of the diagonal band of Broca project through the dorsal fornix to all CA fields of the dorsal hippocampus and adjacent subicular cortex. Other fibers from this region project through the stria medullaris to the medial and lateral habenular nuclei, the paratenial and anteromedial nucleus of the thalamus, and through the medial forebrain bundle to the pars posterior of the medial mammillary nucleus.
>
> Cells located in the intermediolateral septum also project through the lateral part of the fimbria to all CA fields of the ventral hippocampus and adjacent subicular and entorhinal cortices. These cells also send fibers through the stria medullaris to the lateral habenular nucleus and mediodorsal thalamic nucleus. Other axons arising from these cells descend through the medial forebrain bundle to terminate in a region dorsal to the interpeduncular nucleus.
>
> The lateral septum is a relay center for connections from the CA3 of the hippocampus to the ventral tegmental area. These connections help link reward signals with the context in which they occur.[6]
>
> Fibers from the most lateral part of the ventral septum (i.e., bed nucleus of the anterior commissure) project through the stria terminalis to the ventral subiculum. In addition, cells located in the horizontal limb of the diagonal band project massively to the pars posterior of the medial mammillary nucleus, the ventral tegmental area, and amygdala."

These unsubstantiated and uncited statements are too general to be useful in discussing the operation of the hippocampal formation.

Another source[62] suggests,

> "Septal nuclei: a group of nuclei found below the front of the corpus callosum, the septal nuclei are usually considered part of the limbic system and have extensive connections with other limbic

[62]https://www.neuroscientificallychallenged.com/glossary/septal-nuclei/

structures. The septal nuclei are thought to be involved with the experience of pleasure, as electrical stimulation of the septal nuclei is reinforcing in rodents."

Note, the human hippocampal formation is inverted compared to that of the rat (Section xxx).

The above texts would suggest the septal nuclei were elements of stage 4 information extraction and not directly associated with memory formation, storage or recall.

## 17.2.5 Dynamics of declarative memory–learning, recall and forgetting EMPTY

[xxx Chap 9 of Baars & Gage (2007) on learning and memory needs to be incorporated into this chapter. Includes amnesia as well ]
[xxx the configurations of Rudy in his chapters 10 & 11 need to be incorporated in this sec. ]

There are many concepts concerning the dynamics of learning and memory storage at the present time. Rudy (2008) listed at least five theories of perception comparison with previous memories.

| | |
|---|---|
| 1. Consolidation Theory (1900) | Page 133 |
| 2. Active trace Theory (1979) | Page 217 |
| 3. Reconsolidation Theory | Page 218 |
| 4. The Indexing Theory of Episodic Memory (1971) | Page 257 |
| 5. The Standard Model of Systems Consolidation (1984) | Page 284 |
| 6. Multiple trace Theory (1997) | Page 290 |

These theories appeared initially in the psychology community and all appear to rest primarily on partial (minimalist) descriptions of the neural system. Detail related to these theories are few and far between. Rudy has apparently listed them in approximate order of their appearance.

Sternberg[63] has long worked in memory recall and presented an excellent overview ca. 1975. Gazzaniga et al[64]. have cited some examples of Sternberg's ideas.

### 17.2.5.1 Comparison of previous memories and current perceptions

**Figure 17.2.5-1** describes a portion of one concept of the dynamics of declarative memory, called the Standard Model of Systems Consolidation. It involves a mechanism described as medial temporal hippocampal (MTH) system. The concept relies upon a differencing between the current abstract image of the environment and previously stored abstract memories of the same or similar environment. The two memories must be in abstract (non-topographic )form since the perspective used to acquire the two data samples need not be the same. It is also likely that the two abstract images do not preserve "color" information in the broadest since of the word (such as the "color" associated with a somatosensory modality stimulus).

In the example illustrated, the new memory trace must be compared to the old memory trace. After the comparison, wherever it occurs within the neural system, the new abstract memory trace should either 1) replace the previous stored trace, 2) be stored as a new trace identified as a separate perception of the environment previously in memory, or 3) be returned to the process of evaluating unrecognized stage 4 perceptions as a new record of the environment.

This process within the Standard Model must bring the two records to the same engine(s) in order to perform the comparison. In this context, just bringing the indexes together for comparison, whether in the hippocampus or elsewhere, does not appear to be adequate.

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[63]Sternberg, S. (1975) Memory Scanning: New Findings and Current Controversies *Quart J Exp Psych* vol 27, pp 1-32

[64]Gazzaniga, M. Ivry, R. & Mangun, G. (2014) Cognitive Neuroscience: The Biology of the Mind, 4th Edition. NY: W. W. Norton pages 76-78

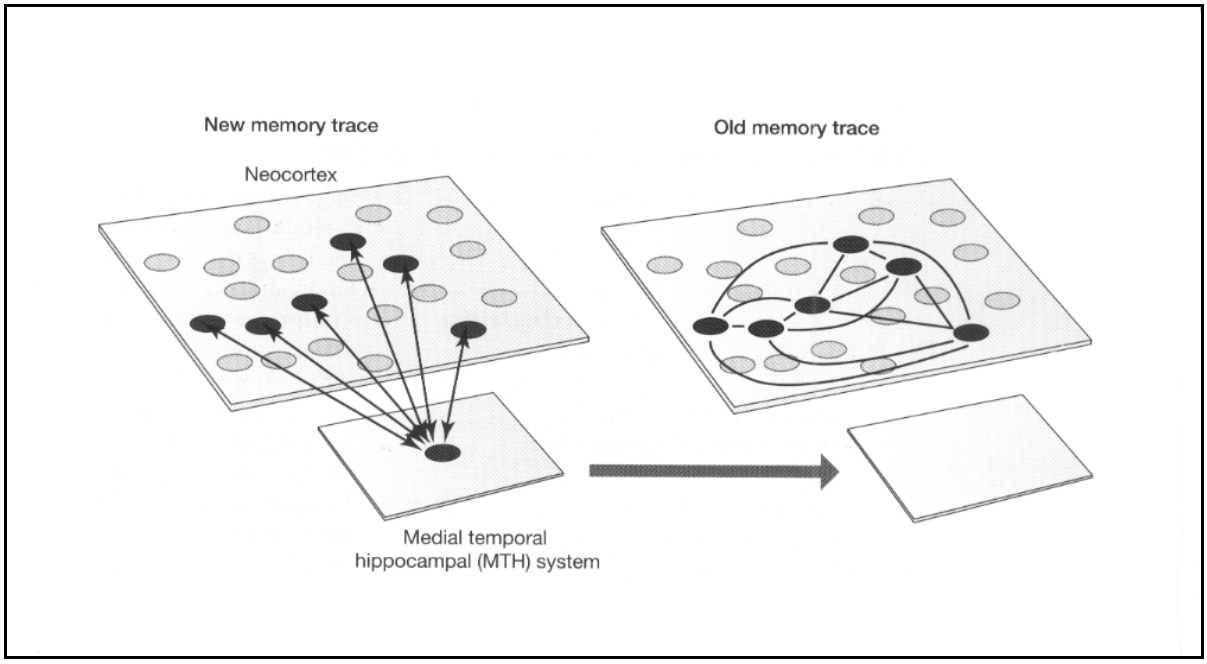


**Figure 17.2.5-1** Schematic of the standard model of systems consolidation ADD. From Rudy, 2008.

### 17.2.5.2 Reaction time in visual matching–Sternberg, 1975 ADD xxx

Sternberg has studied the recall time in visual matching and speculated on many potential forms of serial and parallel memory search. It is not obvious his results apply to a broader assumption of a searchable database. His Introduction opens with,

> "Human memory has traditionally been studied by examining how and when it fails-by considering the frequency and pattern of errors in recall or recognition. These errors may result from failures of learning, retention, or retrieval, and one difficulty in the traditional approach is the disentangling of these alternative sources of error.
>
> During the past decade a complementary approach to the study of memory has become increasingly popular. Here memory is examined under conditions in which it functions successfully and produces performance that is virtually errorless."

Section 5 of his paper requires very careful study due to the complexity of the options discussed. xxx

### 17.2.5.3 Ribot's Law of memory updating EMPTY

An early law adopted by the psychology community dates from Ribot in 1881.

> "Ribot's law of retrograde amnesia was hypothesized in 1881 by Théodule Ribot. It states that there is a time gradient in retrograde amnesia, so that recent memories are more likely to be lost than the more remote memories. Not all patients suffering from retrograde amnesia report the symptoms of Ribot's law." In more modern times, a broader set of recognized causes of amnesia have led to a more refined statements of Ribot's Law. The retrograde character of this disease is not taken to be a smooth function of time. Different causes of amnesia may be associated with different recovery rates. if any.

Page 298 of Rudy (2008) describe challenges to the interpretation of Ribot's Law as he described it.

### 17.2.6 Disorders of the declarative memory

Kopelman has presented an extensive invited review on "Disorders of Memory" from a clinical perspective[65]. He was careful to define his terms. His focus was on "patients with disorders of episodic or semantic memory." He starts off defining amnesia as a syndrome quoting Victor (1971), 'An abnormal mental state in which memory and learning are affected out of all proportion to other cognitive functions in an otherwise alert and responsive patient.' He defines the related Korsakoff syndrome using the same words and adding "resulting from nutritional depletion, notably thiamine deficiency."

[xxx review the rest of Kopelman ]

As noted in **Section 15.4**, disorders related to memory are becoming defined more precisely with the advent of non invasive neural imaging techniques.

A report by Spiers in Zillmer and Spiers is an important example, with citation. It describes in some detail the significant damage to memory resulting from a small injury to the thalamus[66].

#### 17.2.6.1 Amnesia and its extent BRIEF

Squire & Kandel have provided a very brief description of attempts to evaluate amnesia using animal models. See **Section 15.4.1**.

#### 17.2.6.2 Alzheimer's Disease, its potential association with Down's Syndrome etc.

Ingram has presented a recent book interpreting the current scientific data base for the popular audience[67]. There are many anecdotes, some with citations, such as the fact the hippocampus is critical to the formation of long term memory but is apparently not involved in the storage or recovery of such memory. He discusses the histological record of the plaques and tangles found in the brain upon autopsy. As Ingram notes, the difficulty of investigating Alzheimer's Disease is the "contrariness of Alzheimer's, where you expect the disease and it doesn't show or where you don't and it does." He notes the inadequacy of recent (1980's to at least 2010) current reporting on research in genetics (page 172).

> "I don't want to wander too far from the DNA-protein relationship, but it has be be said that much of our DNE doesn't actually bother with all this. A mere 2 per cent is ddicated to protein production, while the rest is involved in regulating the 2 per cent or ensuring that the entire, vast mechanism is chugging along properly. This 98% used to be called junk DNA, but I never actually met scientists back then who claimed that junk DNA didn't do anything. They just didn't know what it was doing."

Ingram notes the effort to correct an imbalance in the concentration of acetylcholine by introducing lecithin (with the current IUPAC name of choline phosphoglyceride). Choline phosphoglyceride (earlier, phosphatidyl choline) is the predominant molecule in the external bilayer of the lemma of all cells and neurons. Why a researcher would attempt to correct an acetylcholine imbalance with the significantly different structure of choline phosphoglyceride is difficult to rationalize. It was probably because of the archaic concept that acetylcholine was a neurotransmitter involved in synaptic signaling.

Ingram's comments relating to the hippocampus are interesting and probably more relevant to research (page

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[65]Kopelman, M. (2002) Disorders of memory *Brain* vol 125, pp 2152-2190

[66]Zillmer, E. & Spiers, M. (2008) Principles of Neuropsychology. US: Wadsworth pg 159

[67]Ingram, J. (2016) The End of Memory. Op. Cit.

93).

His discussion of the "plaques and tangles" situation hints at an observed feature at autopsy that may not be relevant. After describing the initial observations in 1906 by Alzheimer, he notes the significant, devastating, loss in nerve cells in the subjects brain. Ingram defines plaques as "dark spots scattered among the remaining nerve cells." He also describes "tangles"—twisted filaments, aggregates of stuff inside the brain cells." Ingram notes, "They were residues, sometimes the only evidence that told Alzheimer a neuron had been there before." Ingram then spends several pages describing the complexity of the problem of what could be the cause of Alzheimer's Disease.

Ingram's book is a *must read* for anyone wanting to understand where research into this disease stands now.

## 17.2.6.3 Statistical data on memory loss with age

Squire & Kandel reviewed a limited amount of data related to memory recall versus age. They cited a 2001 report by Davis, Trussell and Klebe[68] involving 469 healthy people aged 20 to 89. **Figure 17.2.6-1** reproduces one of their figures. Note the truncated scales. These investigators xxx xxx.

They noted, "The problem is not memory per se, because most people can easily report six digits presented in sequence to one ear. The problem is in processing information presented simultaneously to xxx

It is not obvious how much of a loss in recall can be tolerated by the individual before they become aware of this reduction. The loss in recognition is probably not noticed by the individual until well into old age.

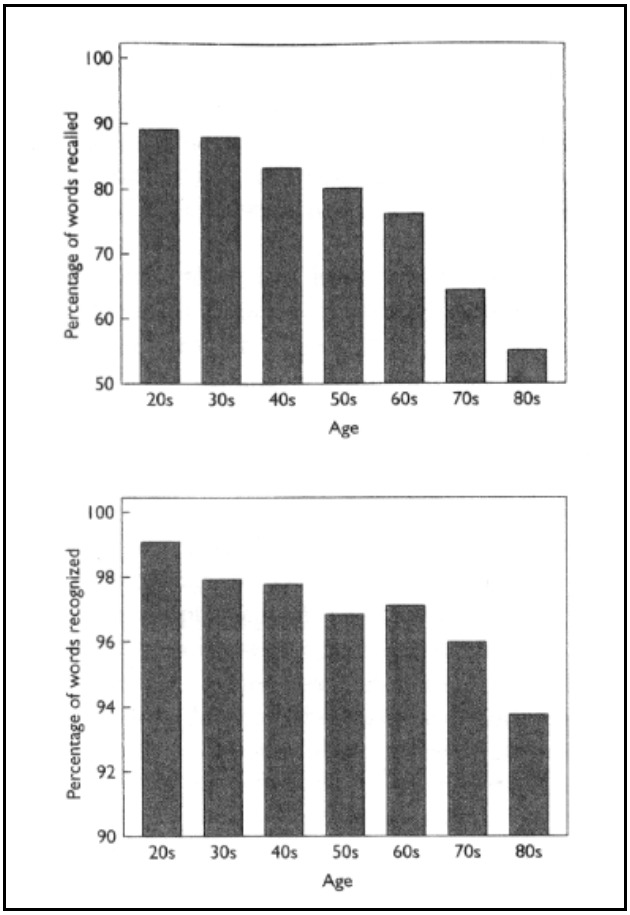


**Figure 17.2.6-1** Performance of 469 individuals on two parallel tests of recall and recognition of words. Subjects were tested 20 minutes after learning. Note the truncated scales. The performance of people in their seventies and eighties is dramatically weaker than that of younger people on the recall test (top). By contrast, there is much less of an age-related difference on the recognition test (bottom). See text. From Davis et al., 2001.

## 17.2.6.4 Clinical observations of GW, a 90 year old female associate

I have known an associate for over five years. She began reporting the loss of taste and smell perceptions about 2.5 years ago. More recently (during the last 12 months. ending in Oct 2017), she has begun reporting the loss of short term memory. Currently, it is easily observed that her short term episodic form of declaratory memory has deteriorated significantly. She cannot remember where she placed an object within the last hour and will proceed to look for it in locations that she has historically placed it. She can still drive distances of 6–10 miles over courses well established in long term memory, but

[68]Davis, H. Trussell, L. & Klebe, K. (2001) A ten-year longitudinal examination of repetition priming, incidental recall, free recall, and recognition in young and elderly *Brain and Cogn* vol 46(1–2), pp 99-104

will become lost if she deviates from that well established course. Her carriage of a cell phone is essentially mandatory at this time in order to obtain help in navigation. Her long term episodic memory has also deteriorated to the point she cannot remember significant events of two years ago. With prompting, she can discuss such events but only superficially. Other elements of her personality remain fully functional at this time. She reads the Wall Street Journal avidly every day. How much she remembers or understands is not known.

GW has not shown any day-to-day differences in her recall related to recent episodic memory, but has exhibited week-to-week differences. Recently, she was taking prepared food to her daughter's home. She got in the passenger seat of a car and set some food on her lap. Within ten minutes, she asked te driver to confirm we loaded the food into the car, in spite of her holding the food in her lab.

## 17.2.7 Reviews of related literature

### 17.2.7.1 Comparison with Buzsaki of 2006

The Buzsaki book of 2006 is a very comprehensive work from the perspective of a clinician specializing in non-invasive exploratory techniques and studying the associated works of others in order to establish an overall understanding of the neural system.

He makes the assertion in one of his section headings (page 285), ""The Hippocampus Is the Neocortex's Librarian," without defining what portion or type of memory he is discussing. Based on the framework of **Section 17.1.2**, it appears the remark only applies to episodic memory within the declarative memory context.

Not to disparage the work but to quantify its context, on page 4, he cites Berger[69] (1929) and notes,

> "The larger deflections measure at most 150 to 200 microvolts. . . ." In other words, the electrical field generated by millions of discharging neurons in the cerebral cortex is 10,000 times smaller than that provided by an AA battery."

His use of ellipses requires further discussion, Berger was either measuring a field strength in microvolts/meter using MEG or the reported voltage range was an indirect measurement such as measured with an electrode on the scalp or introduced into the tissue enclosing the cranium and measuring the cumulative voltage due to the electrical field generated by a large number of neurons at a remote distance. In either case, the analogy to a AA battery is imprecise and suggests a problem in understanding the electrolytics of the neural system. A typical action potential has an amplitude of approximately 100 millivolts, not microvolts, when measured directly and conductively at its axon or using patch-clamp techniques at the same axon.

Buzsaki describes the Fourier Transform in some detail. On page 105, he notes,

> "Because brain signals contain multiple frequency components, their relationship can be quantified using frequency domain methods. The complex EEG or MEG waveform can be reproduced by an appropriate combination of sine waves."

It is not clear whether Buzsaki is aware that the Fourier Transorm allows any recorded EEG or MEG waveform to be reproduced by an appropriate combination of *orthogonal functions*, whether they are sine waves or not. On page 106, he also discusses a "short-time Fourier transform and the technique of "wavelet analysis." It is not clear whether he is actually speaking of the technique more generally known as the fast Fourier Transform (FFT) widely used in electrical engineering. His assertion in footnote 35 that Fourier transforms and Hilbert transforms are identical needs to be analyzed further.

On a different subject, Buzsaki notes,

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[69]Berger, H. (1929) Über das elektrenkephalogramm des menschen *Euro Arch Psych & Clinic*

## 58 Neurons & the Nervous System

> "In autoassociative attractor networks, the maximum number of stored memories is limited by the decimal order of the number of converging synapses on a single cell from other cells. If memories are stored by static anatomical connections only, the upper limit of the number of memories that can be stored in the rat hippocampus would be tens of thousands, and the storage capacity may not increase much more as we go from rat to human." with citations and further discussion.

Clearly, this is not the order of memory volume we are concerned with in this work. On page 34, Buzsaki states;

"The most prevalent neuronal type of the cerebral cortex, the pyramidal cell, has 5,000–50,000 postsynaptic receiving sites."

Actually, as he notes on page 291 in the same paper, the granule cells outnumber the pyramid cells by a factor of between 20:1 and 50:1.

He goes on to examine search strategies in a philosophical discussion,

> "Let's begin with some theoretical speculation." and later in the paragraph, "Construction of a full random graph from 200,000 CA3 pyramidal cells would require only 15–20 divergent connections from each cell. However, going from any neuron to any other neuron may require an excessively large number of steps (i.e., long synaptic path length, as referred to in Cycle 2). The theoretical minimum of 10–15 connections is in stark contrast to the 10,000–20,000 synapses that an average CA3 pyramidal cell establishes with its peers. With this large divergence, in principle, activity can jump from any neuron to any other through just two synapses. Furthermore, the large divergence implies that the number of possible routes between any randomly chosen start and goal cell is a truly galactic figure. Nevertheless, no matter how impressive this figure is, we do not get far with such anatomical reasoning alone, because synapses between pyramidal cells are weak, and the discharge of a single starter cell will not be able to fire any of its target peers. Yet, only discharging neurons can be used for encoding and retrieving memories."

There is much food for thought in these statements. In a following paragraph he introduces "granule cells" without describing their detailed characteristics. In fact, his pyramid cells are stage 3 encoding and decoding neurons and his granule cells are stage 2 analog neurons. His autoassociator is the equivalent of the associative correlators of this work (See particularly Chapter 8 of "Hearing: A 21st Century Paradigm".

> "Distribution of the input in the large space of the autoassociator requires a special mechanism, and this is where granule cells become critical. Each superficial entorhinal neuron receives inputs from large neocortical areas. In turn, an estimated 50,000 layer 2 stellate cells send inputs to 1,000,000 granule cells, each of which is a recipient of inputs from approximately 10,000 converging entorhinal neurons. Viewed differently, a single entorhinal stellate cell disperses its information to 20 times more granule cells. The goal of this arithmetic exercise is to contrast the large fan-out in the neocortex–entorhinal cortex–granule cell axis with the exceptionally low divergence and convergence of the granule cell projections to the CA3 recurrent system. An average granule cell contacts only 20 CA3 pyramidal cells, a mere 0.1 percent of the possible targets. Because of this low divergence, fewer than 50 granule cells converge on a single pyramidal cell."

On page 292, he addresses another important subject,

"How to Study the Mechanisms of Explicit Memory in Animals?

A major conceptual difficulty of studying the mechanism of memory storage involves the exclusive nature of memory definition. Episodic memory is claimed to be uniquely human, a mental travel back in time that endows the individual with the capacity to reference personal experiences in the context of both time and space. It is these life-long experiences, representing unique events through spacetime, that give rise to the feeling of the self and are the sources of individuality. The singular episodes can reemerge through the process of free recall. Semantic
knowledge, on the other hand, is largely a context-free form of information. It is the "meaning" of things. Against this background, how are we expected to work out physiological mechanisms of declarative memories in animals simpler than humans?"

He provides no citation for limiting episodic memory to humans. Elephants and many other animals are known to exhibit significant episodic memory.

He also addresses the potential methods of navigation in two-dimensional space. He restricts most of the discussion to 2D because most of the available research relates to mice and other small rodents who live in a largely 2D environment (at least in the caged laboratory).

### 17.2.7.2 Remarks re Squire & Kandel, 2nd Ed., 2009

As noted in the introduction, this 2nd edition contains much introductory material in chapters 1, 2 & 3 that can be(must be) ignored. It is thoroughly dated, cites a number of researcher's hypotheses that have not been expanded upon since initially enunciated, nor confirmed or accepted by the broader community as relevant. Much of chapter 3 includes similar material, however figure on page 60 may apply to the interface between a stage 6 command neuron and a orthodromic motor cell. It does not apply to an interneuron interface. Most of the discussion related to a long list of complex chemical reactions at a synapse remain conjectural to this day, without significant demonstration of the reactions and residues of these conceptual reactions at a neuron/neuron interface.

As of page 70 (out of more than 250), the book has not provided any block diagram, schematic or other graphic description of the neural system dedicated to memory. **Section 17.1.1** and **Section 17.1.2** of this work provide such initial block diagrams. The second citation was generated based primarily on the earlier work of Squire & colleagues cited there. Page 77 makes several assertions related to the storage of declaratory memory that do not appear consistent with the 21st Century literature related to the hippocampus derived from MRI investigations. However, the wording of these assertions appears more conceptual than detailed. They do note, "there is still no technique that allows one to pinpoint a memory directly in the mammalian brain; we cannot as yet locate the sites where memory of some particular object is stored." This is largely because we do not yet know what form of coding is used to store the memory. Squires & Kandel reiterate the earlier concept that a given memory is stored as an engram (a modification of the concept of an n-gram, an n-dimensional signature). Their subsequent discussion of the engram is largely conceptual. They discuss retrieval of declaratory memories, the forgetting of declarative memories, and the imperfections in declarative memory in similar conceptual language.

Chapter four contains considerable discussion based on largely on concept obtained from observing patient behavior, with or without substantial trauma to the patient's neural system. Separate sections are provided addressing;

– Storing Declarative Memory,
– Retrieving Declarative Memory,
– Forgetting Declarative Memory,
– Imperfections in Declarative Memory.

No discussion of how declarative memory is stored or accessed from a functional circuit perspective is provided. No discussion of where or in what format/coding memory is stored.

Chapter five provides a foundation for discussing short-term memory, immediate memory and working memory. Immediate memory is described in terms of the ability of the average person to remember a nominal 7 digit (telephone) number for less than 30 seconds unless it is "rehearsed." The term rehearsed was not further defined at that point but appears to involve actively repeating the immediate memory in the conscious mind over a period of time. This rehearsal causes the information to be remain in working memory for a longer period and the information may be transferred from there to long-term memory. The paths and mechanisms of these transitions remain undefined. The text then proceeds to a discussion of long-term memory and the transition from immediate to long-term memory. Amnesia is also addressed in chapter five. General comments are included as to the properties of declarative memory. Several "puzzling" examples of memory capability were included with references to the role of the hippocampus. Brief remarks are included relating to the temporary role of the medial temporal lobe in memory followed by introductory remarks concerning both episodic and semantic memory. "Both episodic and semantic memory are declarative. Information is retrieved consciously and subjects are aware that they are accessing stored information." See **Section 17.1.2**. [xxx add definitions here ] They did discuss a patient, H. M. from a behavioral perspective after suffering an ischemia in the vicinity of the area labeled CA1 of the hippocampus. After others developed

an animal model believed to replicate the human with regard to amnesia, they assert that in amnesia, skill-based memory and immediate memory are spared.

Squire & Kandel do not recognize or describe any separation between the peripheral retina/LGN/occipital lobe signal path and the foveola/PGN/pulvinar signal path. As a result, their brief discussions of the role of the temporal and parietal lobes in memory are quite limited. They do not identify or define any saliency map. The book does not introduce or discuss non-declaratory (implicit or procedural) memory and the role of the cerebellum in support of non-declaratory memory. Squire & Kandel provide a very brief description of the state of the art related to understanding amnesia (pp 105-108).

Chapter six discusses potential synaptic storage mechanism for declarative memory based on their reliance on the chemical theory of the neuron and synapse. They provide a highly conceptual description of the role a synapse might play in memory. It involves the development of a very chemically complex presynaptic region at a point along an axon that is adjacent to a similarly complex neurite designed to accept chemical neurotransmitters. This work defines a much simpler synapse that only requires the physical elaboration of a bouton on the axon segment adjacent to a target neurite, thereby creating a pedicle of the axon segment that is within the small physical distance of the dendrite required to achieve "semiconductor action." This action then constitutes an "active diode" supporting the flow of electrons between the axon segment and the target neurite without further physical elaboration of the chemistry at that point.

Chapter seven includes an interesting but highly speculative aside, concerning how the storage of memory might involve changes in the DNA of a cell.

> "How genes are switched on and off is a fascinating and important topic. Fully one-fifth of *all* genes in the human genome—about 5000 genes— encode transcriptional regulatory proteins, both activators and repressors, that regulate the expression of other genes!" The emphasis on *all* and the exclamation mark punctuation was in the original text.

Squire & Kandel went on to review the work of two French scientists who won a Nobel Prize for their work in this area in 1965. Squire & Kandel drew few conclusions about the potential changes in DNA could be caused by neural signals traversing any elements of the Limbic System.

Chapter ten includes a brief discussion (pages 220-227) of the potential causes of Alzheimer's Disease (relying on the conventional wisdom relating to plaques as of 2009. By 2017, after the expenditure of vast amount of clinical research, most of it carried out on patients post mortem, the role of plaques as a cause in Alzheimer's Disease is rapidly fading in favor of other causes. The focus is moving to the amygdala and hippocampus rather than the cerebrum. They discussed the amygdala and hippocampus from a morphological perspective in chapter 5, but did not discuss their mode of operation.

## 17.2.8 Speculation concerning stage 5B & 5C operation EMPTY

It is appropriate to begin differentiating between the three identified portions of stage 5,

5A: The analytical (including the intellectual) portion of cognition, associated with the Awareness Mode of neural operations.
5B: The emotional (Limbic engines) portion of cognition associated with the Alarm Mode of neural operations,
5C: The memory portion of cognition associated with a variety of types of memory supporting stages 5A and 5B.

It is also now appropriate to begin differentiating between activities associated with the Alarm Mode and the Awareness Mode at the stage 5 Cognition level.

Finally, it is appropriate to recognize the limited ability, if any, of the amygdala to transfer any information to long-term memory in the cerebellum.

**Figure 17.2.8-1** is provided as a preliminary graphic expansion of stage 5 cognition activity to account for these assertions. Price identified the monodirectional path beginning in CA1 of the hippocampus and ending in the "frontal cortex" based on Carmichael & Price (**Section 4.6.3.1**).

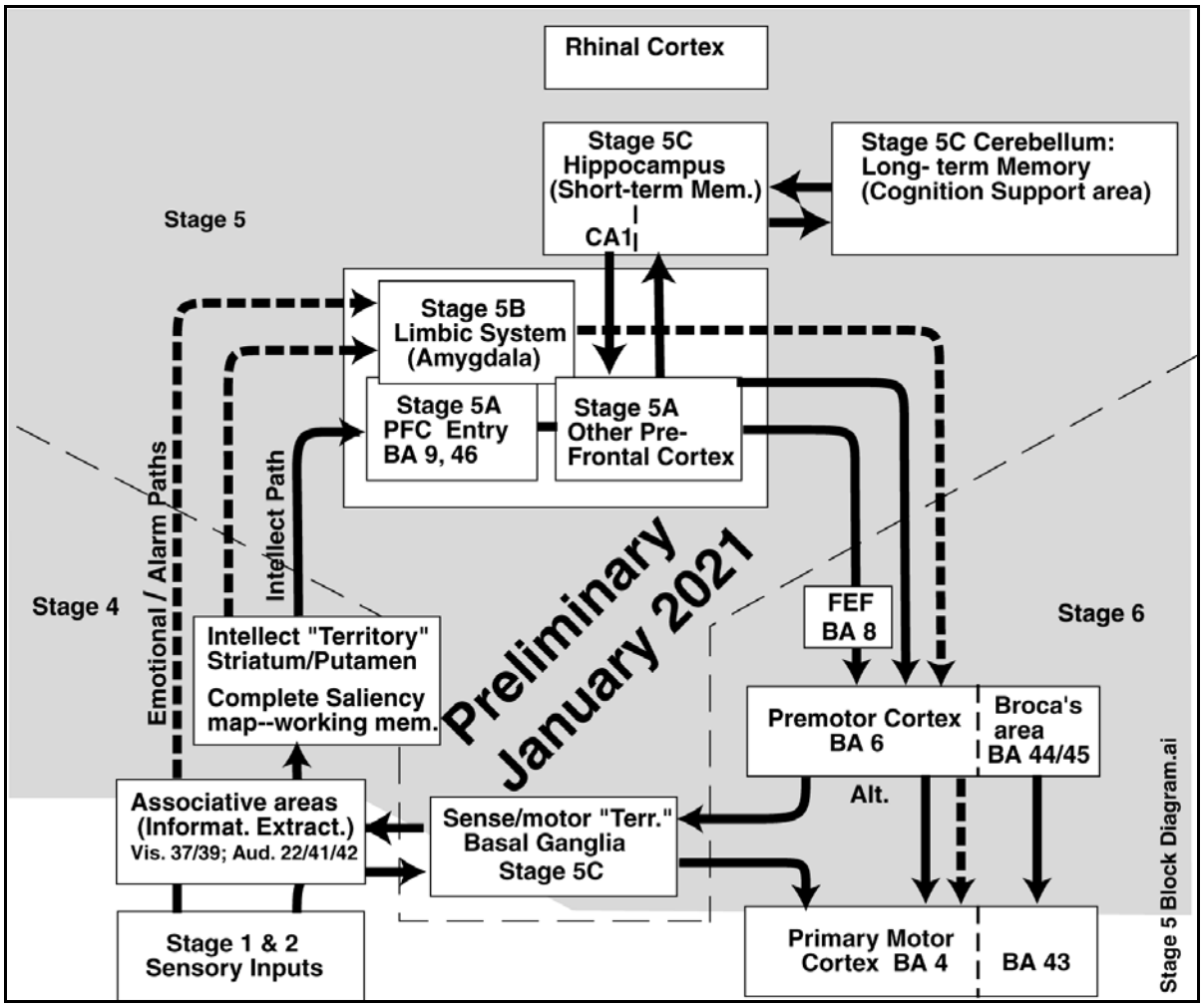


**Figure 17.2.8-1** Preliminary expansion of the stage 5 top level block diagram into 3 portions. Price has identified the path from CA1 of the hippocampus to the "Frontal Cortex" of stage 5A.

Rudy (2008, page 244) introduced exploratory research suggesting that the amygdala and hippocampus were less involved in episodic memory than previously thought based on Squire (1987). The implication was that the Rhinal Cortex may be more significant in capturing and/or recalling episodic memory (See also **Section 17.2.3**).

### 17.2.8.1 Speculation on the character of signals within the hippocampal path

**Figure 17.2.8-2** presents a proposed hippocampal memory loop for discussion. Note the similarity of elements in the figure to the above figure from Squire & Dede.

**Section 17.5** will address the dynamics of memory based primarily on the model presented in this section.

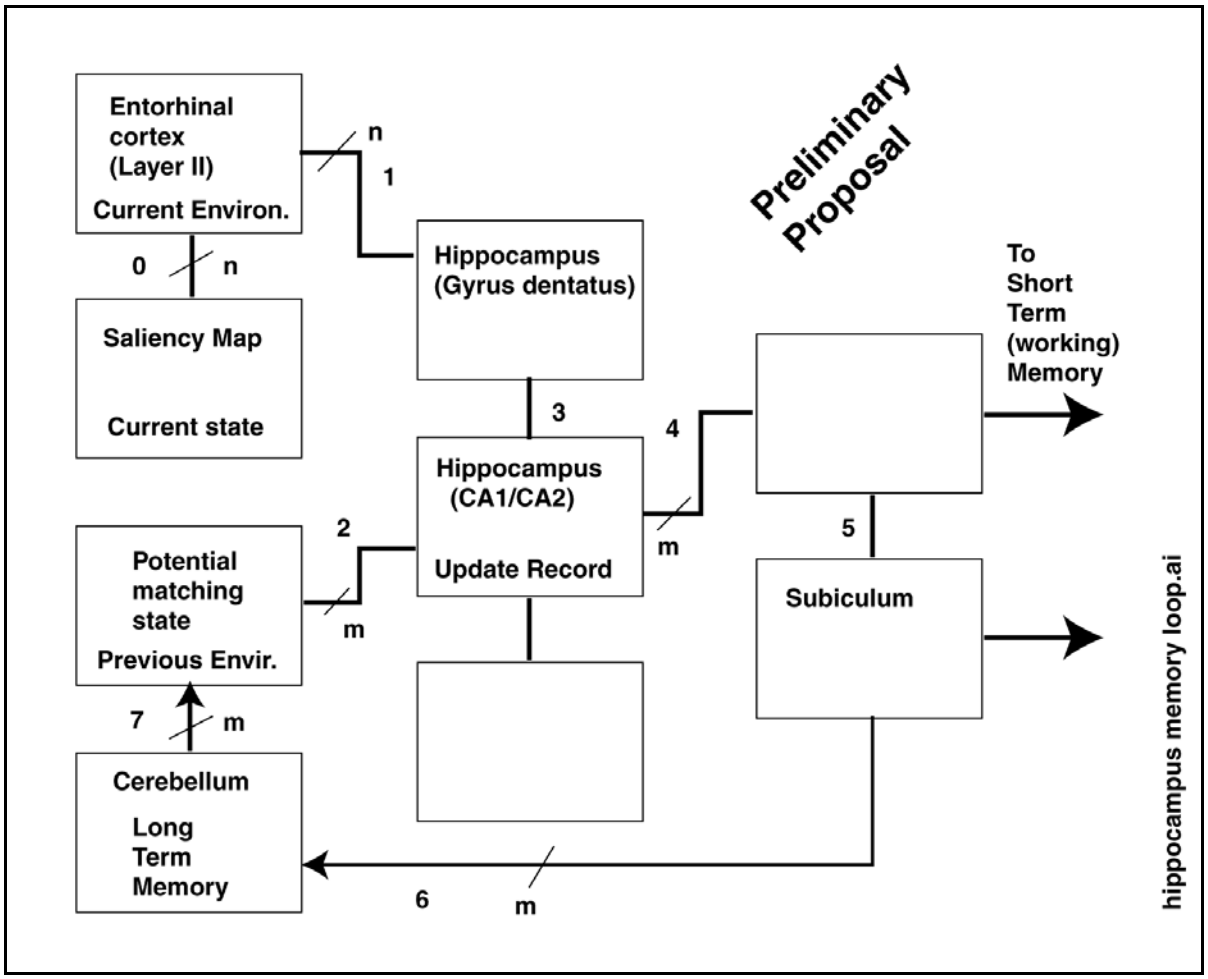


**Figure 17.2.8-2** Candidate hippocampal memory update loop. The loop operates generally in numerical order beginning with zero. Each of the neural paths consists of multiple stage 3 neurons constituting a fascicule. The neurons of a fascicule are proposed to be transmitting their signals in word serial/bit parallel form using the same encoding as in other stage 3 neurons. $n \geq m$. All of the signal projected around the loop are proposed to be in an abstract (non tonotopic) form. See text.

### 17.2.8.2 Speculation on the character of signals between the Stage 5B hippocampal formation & the CNS

As noted in the first paragraph of **Section 4.6.3**, to coordinate more recent investigations, such as presented in this **Section 17.2.2**, stage 5 has now been subdivided into three parts.

Stage 5A relates to logical cognition via the prefrontal cortex.
Stage 5B relates to emotional cognition via (parts of) the Limbic System.
Stage 5C relates to memory directly supporting stages 5A and 5B.
[xxx confirm sequence
**Section 7.1.3** will also be modified to support this nomenclature.

When exploring the anatomy and architecture of the CNS, it was frequently noted that researchers seldom suggested that the cognitive engines of the CNS were associated with emotionally charged information

extracted from the stage 4 engines of the CNS. On the other hand, investigators (particularly in the clinical environment) frequently discussed associated emotionally charged situations with the Limbic System and more specifically the hippocampal formation. These considerations led this investigator to speculate whether, what had previously been labeled the stage 5 cognitive engines of the CNS, generally described morphologically as the prefrontal cortex, PFC, might be accompanied by a separate stage 5 element that might process such emotionally charged stimuli.

Merging the (primarily morphological and traffic analysis terminology used by the Yassa Lab, Duvernoy, and Felten & Shetty with the previous discussions in this work is a challenge. The prior traffic analyses have been limited primarily to descriptions of the prevalence of neurons connecting pairs of engines within the hippocampal formation. It has not presented data on the volume of signals over these paths per unit time, or to the number of neurons in a given fascicle connecting such pairs of engines. As noted in **Section 4.6.6**, the Yassa Lab described a circular signal path without any focus on a significant input or output path. With a few exceptions in his chapter 3, Duvernoy did not provide any drawings detailing signal paths (**Section 10.2.5**). The signal paths were described in text form that can be easily misinterpreted and are generally not sufficiently exclusive. His focus was on anatomy, morphology and histology. Felten & Shetty provided more graphical descriptions of signal paths but at a gross level (**Section 17.2.2** and **Section 17.2.3**).

Looking more closely at **Section 4.6.3** and the figures therein, it was noted that the section of the cerebellum labeled stage 4b, might be presented emotionally charged information from the earlier engines of stage 4, that the cerebellum might present its findings to the association areas of stage 4, via the thalamic reticular nucleus (TRN) operating in its “control and switching” role, After the engines of the association areas completed their processing, they might establish an area (possibly distinct from the dedicated sensory areas) in the saliency map describing the perceived emotional atmosphere of the external environment. This distinct area might be accessed by a dual of the logical cognitive engines of the PFC, comprising the emotional cognitive engines of the Limbic System, labeled stage 5B.

If emotionally charged information is presented to the stage 4b cerebellum, but it is not recognized, then the system as defined in the previous paragraph reverts to the learning mode, similar to the one also described in **Section 4.6.3.** Learning can be described by the circular arrow below the label, “Limbic System” in stage 5B. It is a slower loop that depends on the Limbic system to interpret the emotionally charged state present in the saliency map and present its evaluation to stage 6b of the cerebellum for updating of its stored records while also instructing the premotor cortex and primary motor cortex to respond to the emotionally charged environment as suggested by the figure.

The challenge here is to more completely define the information paths from the saliency map through stage 5B using the points developed in **Section 17.2.2.1** and its sub-sections. Some of the clinical labels differ from the biophysical labels for the same engine; the thalamic reticular nucleus is frequently labeled the anterior thalamic nuclei in the clinical literature. This structure is actually a thin neural layer enclosing a considerable portion of the thalamus and the source, or way-point, of much of the corona radiata.

**Figure 17.2.8-3** provides a larger proposed scope of the interconnections between stage 5B emotional cognition and the remainder of the CNS. It is modeled after the stage 5A logic cognition circuitry developed in **Section 4.6.3**. This version is a preliminary proposal.

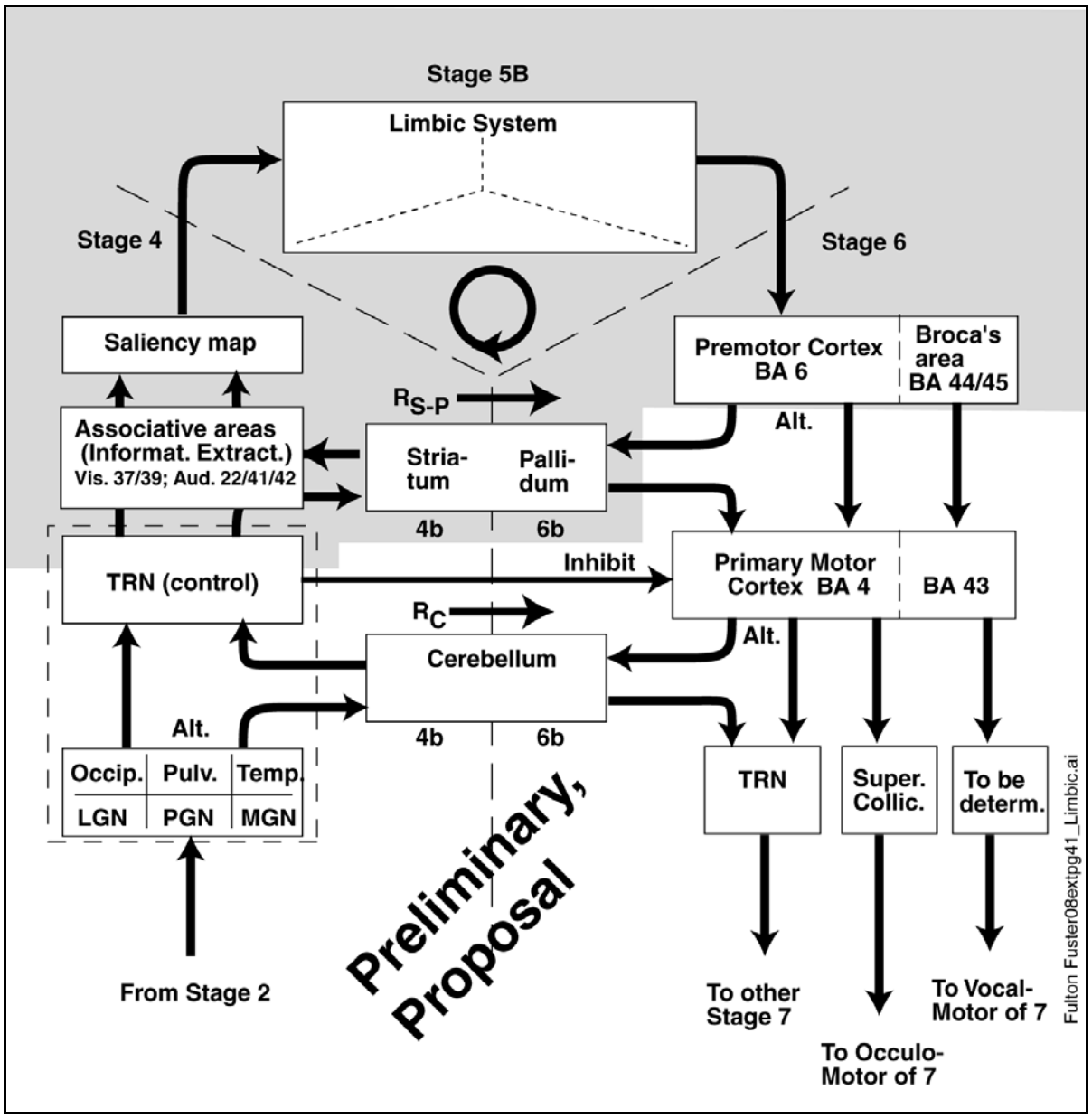


**Figure 17.2.8-3** Proposed interconnections between stage 5B and the remainder of the CNS. The proposal follows the similar graphic for the interconnections of stage 5A logical cognition and the remainder of the CNS in **Section 4.3.6**. The figure attempts to merge the above remarks concerning the Limbic System, stage 5B with the earlier proposals related to stage 5A and the remainder of the CNS. See text. Extensively modified from Fuster, 2008.

### 17.2.8.3 Proposed merging the engines of the Limbic System with the CNS

Merging the material in the previous two figures based on the comments of Felten & Shetty and others in the context of Section 4.6.3 can lead to several schematics for the Limbic System. [xxx expand ]

## 17.3 (Reserved)

## 17.4 Non-declaratory memory EMPTY

McDonald & White[70] have described the potential for three separate non-declaratory memory systems. [xxx add ]

### 17.4.1 (Potential writing of non-declaratory memory RESERVED)

### 17.4.2 (Potential recall of non-declaratory memory RESERVED)

The work in the field of autonomous vehicles is fast developing the field of mapping the course of the vehicle through a dense environment and the ability of the vehicle to retrace its steps *without* addressing each step along the path individually via the application of stage 5A or 5B like cognition. Yet, this mapping can be recalled (as in declaratory memory) at the discretion of the vehicles "brain" or upon request by the controller of the autonomous vehicle.

Thrun & Leonard[71] have provided good background, including graphics, of progress in this area since 2000.

Further analysis in this area may justify defining a type of memory intermediate to declaratory and non-declaratory memory.

## 17.5 The Cerebellum as the focus of all declaratory and non-declaratory memory EMPTY

Mostly because of its size, based on neuron count, and partly because of the recognized small size and lack of any structure likely to support memory formation within the Limbic System, it is common to associate the majority of both declaratory and non-declaratory memory with the cerebellum.

It should be noted that many reflex actions appear to involve memory cells but in actuality, reflex actions merely involve shunts between afferent and efferent paths incorporated into the design of the neural system.

**This Section 17.5 and Section 17.6 will closely track and exchange material with Section 15.8.8 in "Processes in Biological Vision," the Project Vision on the ResearchGate.net site.**

### 17.5.1 Background related to the cerebellum

The study of the cerebellum has gone on for much of the last two centuries. However, it has occurred in spurts, and most of the work of the late 20th Century still depends on the work of Cajol in the late 19th and very early 20th Centuries. As a result, much of the figures displayed in the literature depend on his early figures, at least for inspiration. A **second** major problem is the difficulty of the physical laboratory investigations. The result is research on only a few animals in a given investigation and the resulting small statistical size and a lack of statistically precise measurements. This situation will become obvious in **Section 17.6** *were an attempt is made to focus on a proposed baseline for the 21st Century*. A **third** problem is the sporadic study of the cerebellum. Different groups have focused on the cerebellum at intervals of a few decades. There has been inadequate communications between these groups. To still be quoting the camera lucida sketches of Cajol in the late 20th Century should be an embarrassment to the histological community.

The cerebellum is discussed from a component perspective in **Section 10.2.4.**

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[70]McDonald, R. & White, N. (1993) A Triple Dissociation of Memory Systems: Hippocampus, Amygdala, and Dorsal Striatum *Behavioral Neurosci* vol 107(1), pp 3-22

[71]Thrun, S. & Leonard, J. (2008) Simultaneous Localization and Mapping *In* Siciliano, B. & Khatib, O. *eds*, Springer handbook of robotics. NY: Springer Chap 37 pp871-886

## 17.5.1.1 Interpreting the papers of the Eccles team of the 1960-70's

Eccles and an extensive team of associates and students produced a very large number of papers concerning the cerebellum during the 3rd quarter of the 20th Century. It culminated in a major text in 1967. Much of the discussion and conclusions related to this material is now and must be looked upon as exploratory research. However, it provides a wealth of data of considerable value.

Eccles, Ito & Szentágothai have collected a wide variety of empirical information without resorting to or presenting a model of the electrical circuits involved. Some of their data is difficult to interpret. This is largely due to the fact the measurements were made under grossly abnormal conditions. The cell was excited antidromically, with a pulse applied to the extremity of the axon and observed to travel toward the dendrite of the neuron. The current paths were observed by probing the intercellular space as accessed by a 41 micron diameter (s. w. g. #48) hyper-dermic needle. This needle is significantly larger than the individual Purkinje cell. A typical Purkinje soma is nominally 15 microns in diameter. As a result, the drawings are only crude approximations of the fields generated by actual neural operations. These investigators encountered 100 mV positive going pulses when probing the axon under normal operating conditions (figure 47E & F) and less than 1.0 mV negative going pulses when interrogating the soma area of the cell (figure 45A–D). The negative going pulses are indicative of the poditic portion of the cell. This area connects to or forms the base region of the three-terminal Activa within the cell (**Section 4.xxx**). The waveforms captured by Eccles, Ito & Szentágothai, and other papers by the Eccles team, must be carefully interpreted. They describe the chemicals placed in their probe. However, they do not discuss or illustrate any *electrical compensation* associated with their probe to avoid excursions below their baseline due to inadequate capacitive compensation (**Section 2.10.2.1.3,** comment by Spruston). This is a major oversight on the part of Eccles and team in a wide range of their voluminous published papers of the 1960-70's.

Most of the waveforms in their 1967 text do not qualify as action potentials associated with the myelinated axon of a Purkinje cell. Most are analog waveforms, frequently captured by probing the base of the Activa within the soma of the cell. These waveforms are generally negative going and only a few millivolts in amplitude. The displays are from an early generation of oscilloscopes, predating the era of the Tektronics oscilloscopes that were just arriving in the non-military laboratories.

The nomenclature used is unusual, and definitions are hard to locate in a specific paper. Several important labels are presented in the following brief excerpts.

"Stimulation deep in the cerebellum in the region of the fastigial nucleus (juxta-fastigial, J.F.)"
"When electrical stimuli were applied to the surface of a cerebellar folium by a local electrode (LOC),"
"the mossy fibre-granule cell relay (MGR),"
"The glomerulus in the cerebellar granular layer is composed of the three elements; the mossy fibre terminal, the granule cell dendrites and the Golgi cell axons."

These terms are illustrated in an earlier paper by Eccles, Llinas & Sasaki[72]. Eccles and team were prolific authors such that this work will cite the date of an article with a suffix taken from the Eccle, Ito & Szentágothai text. The Summary of the Eccles, Llinas & Sasaki (1966a) paper reads,

> "1. Extracellular microelectrode recording has been employed to study the responses of three types of interneurones in the cat cerebellar cortex: basket cells, superficial stellate cells and Golgi cells. The large unitary spike potentials of single cells were sharply localized and *presumably* were generated by impulse discharges from the cell somata. The characteristics of their responses described below sharply distinguished them from Purkinje cells.
> 2. The parallel fibre volleys generated by surface stimulation of a folium evoked brief repetitive discharges that were graded in respect of frequency and number. Maximum responses had as many as 10 impulses at an initial frequency of 500/sec.
> 3. At brief test intervals there was facilitation of the response to a second parallel fibre volley; at about 50 msec it passed over to depression for over 500 msec.
> 4. Stimulation deep in the cerebellum in the region of the fastigial nucleus (juxta-fastigial, J.F.) evoked

[72]Eccles, J. Llinas, R. & Sasaki, K. (1966a) The inhibitory interneourones within the cerebellar cortex Exp Brain Res vol 1, pp 1–16

by synaptic action a single or double discharge, presumably by the mossy fibre-granule cell-parallel fibre path, but climbing fibre stimulation from the inferior olive also usually had a weak excitatory action evoking never more than one impulse.
5. J.F. stimulation also had an inhibitory action on the repetitive discharge evoked by a parallel fibre volley. Possibly this is due to the inhibitory action of impulses in Purkinje cell axon collaterals.
6. There was a slow (7--30/see) and rather irregular background discharge from all interneurones. The inhibitory actions of parallel fibre and J. F. stimulation silenced this discharge for some hundreds of milliseconds, probably by Golgi cell inhibition of a background mossy fibre input into granule cells.
7. All these various features were displayed by cells at depths from 180 to 500/2; hence it was concluded that *superficial stellate, basket and Golgi cells have similar properties, discrimination being possible only by depth*, the respective depth ranges being superficial to 250/2, 250/2 to 400/2, and deeper than 400/2." [Italics indicate emphasis added.]

This summary will be referred to frequently below. Many more recent papers condense their discussion to a single label, Golgi cells, in line with item 7 above.

### 17.5.1.1.1 The detailed description of the neurons of the cerebellum

On pages 15 through 31 Eccles et al. struggle to differentiate between stellate, basket and other neuron types, relying upon many electron micrographs to strengthen their case. To a non-histologist, they are not convincing. Whatever names a cerebellum investigator chooses to use, the analyst and reader of their work must accept the labels the investigators use and try to fit the functions of the labeled neurons into their own larger context.

The Purkinje neuron of the cerebellum is the exception to the above problem. It is fairly well identified both histologically and functionally (physiologically). This statement is reinforced by the excellent paper of Szentagothai (1965a).

### 17.5.1.2 The anatomy relating to the cerebellum

Until recently, the number of neurons within the cerebellum compared to the CNS was not appreciated. Herculana-Houzel has recently shown that the cerebellum consists of over 75% of the neurons in the CNS **(Section 17.2.2.1**). The numbers of neurons included in the three significant peduncles of the cerebellum is proportionately high. Noback has illustrated these peduncles in his figure 1-8, reproduced here as **Figure 17.5.1-1**.

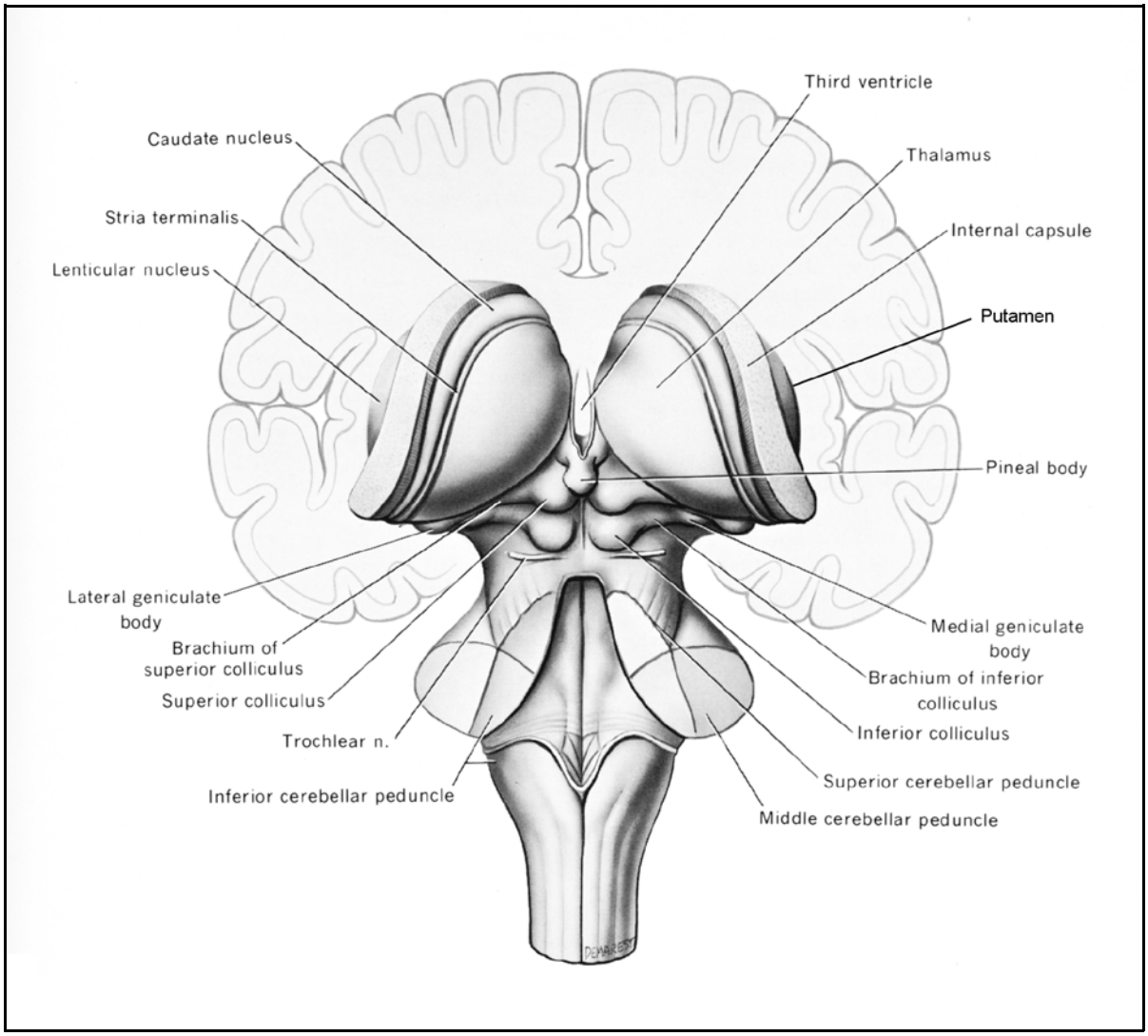


**Figure 17.5.1-1** The three massive peduncles of each hemisphere of the cerebellum. When combined they are larger in cross section than the brain stem shown below them. From Noback, 1967.

Noback has also provided a figure 9-3, reproduced here as **Figure 17.5.1-2**, showing only a minuscule number of the signal paths through these peduncles.

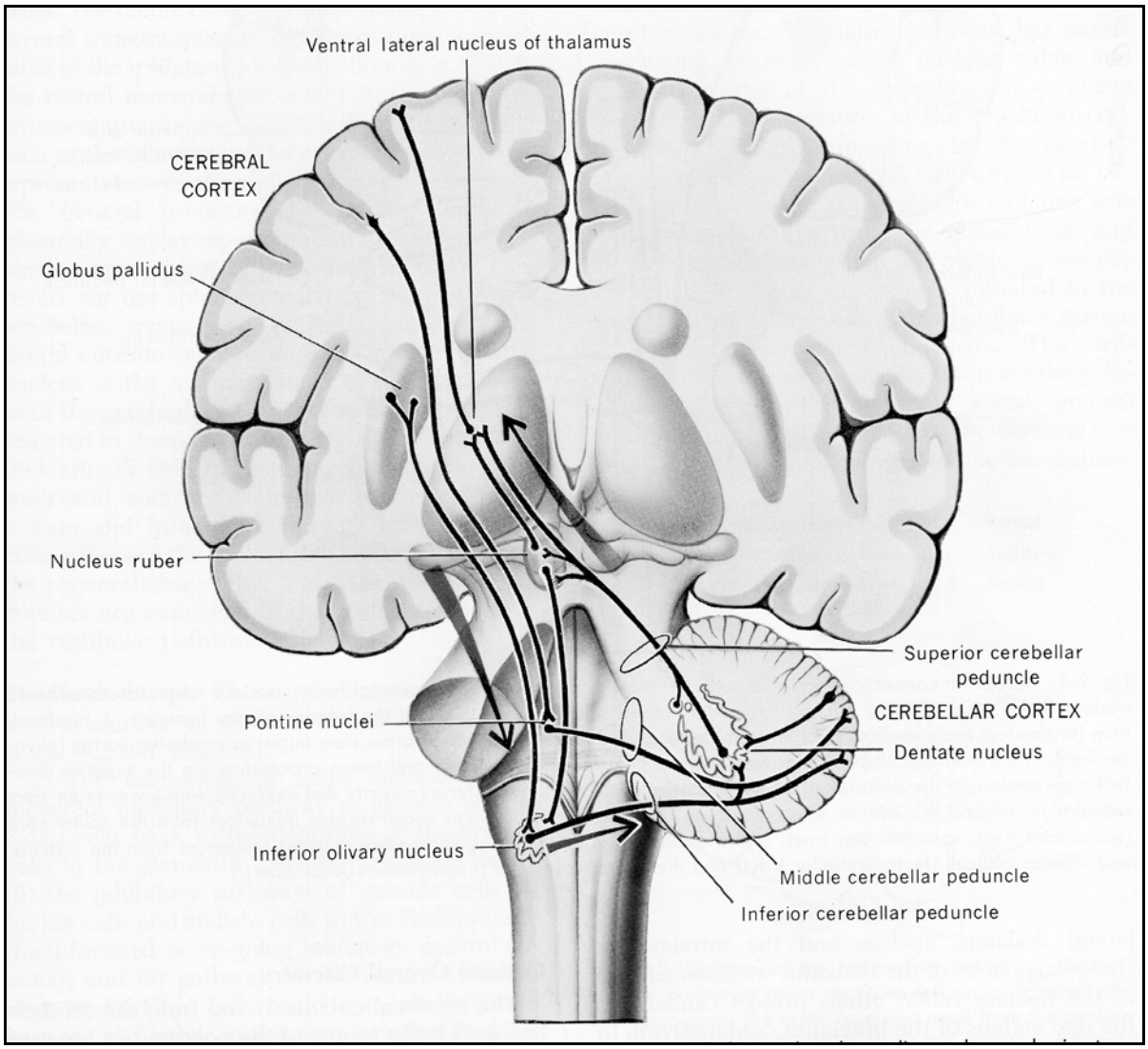


**Figure 17.5.1-2** Showing selected signal paths through the 3 peduncles of one hemisphere of the cerebellum, There are likely to be more than several billion neurons passing through the peduncles of each hemisphere. From Noback, 1967.

### 17.5.1.3 Interpreting the cerebellar cortex atlas of Palay & Chan-Palay

This atlas[73] is quite comprehensive with respect to the cerebellar cortex. It includes both light microscopy and electron microscopy images, as well as statistical data for virtually every structure within the cerebellar cortex.

An amazing finding after reviewing this atlas is the lack of knowledge within the entire neural research

[73]Palay, S. & Chan-Palay, V. (1974) Cerebellar Cortex: Cytology and Organization. NY: Springer-Verlag

community concerning the granule cells of the cerebellar cortex. As late as 1974, there is no agreement as to the number of granule cells. In 1958, Brautenberg & Atwood estimated there were between $10^{10}$ and $10^{11}$, ten billion and one hundred billion respectively, granule cells in human (page 64 in Palay & Chan-Palay). Taking the average of these values, there are 55 billion granule cells in human that have not been studied in any significant manner. Even the small group of these neurons, granule cells forming parallel fibers passing through the dendritic tree of a single Purkinje(estimated to consist of 200,000-300,000 in monkey by Fox & Barnard in 1957[74]), have not been studied sufficiently to understand their operational role (**Section 10.2.4.3.1**). There appears to be a typographical error on page 67 where a value of 2.0 microns from a Palkovits et al. paper (1971c) is compared favorably with a value of 1.6 mm for the average length of parallel fibers in cat (probably the correct measurement).

In essence, almost one-half of the neurons in the human brain, the vast majority of the neurons in the cerebellum, at a count of about 40 billion cells, ***as to their operating mechanisms are unaccounted for in the scientific literature*** as of 2017 (69 billion or over 75% of the total CNS count as of 2020, **Section 17.2.2.1**). Whether the parallel fibers are acting as indices to select specific Purkinje cells (or multiple cells), **or** are carriers of actual signals (information) is still in debate. The majority of these granule cells are too small to be studied effectively using light microscopy (although some advances are being made in light microscopy). Most of their neurites have diameters below the diffraction limit of typical visual microscopes. The axons are similarly small. Following their bifurcation, the resulting parallel fibers are wrapped in only a few layers of myelin (Palay & Chan-Palay, page 88). Page92 of their atlas shows the crystal-like packing of the parallel fibers at x20,000 magnification.

Fox & Barnard made some important assertions in their Introduction,

> "Purkinje cell dendrites have two distinct, morphologically different, receptive regions each with its own specific afferents: the smooth branches, contacted by the climbing fibres, and the spiny branchlets, contacted by the parallel fibres (Cajal, 1895). The former are 'longitudinal axo-dendritic connexions' (Cajal, 1934, 1954), a type of synapse allowing an axon many contacts on the dendrites of a single neuron; the latter are 'cruciform axo-dendritic connexions of great length', a type of synapse permitting the dendrites of each neuron contact with a great number of axons and each axon contact with the dendrites of many neurons. The recognition of two receptive regions in the Purkinje cell dendritic system resulted from Cajal's (1891) discovery of the peridendritic spines, which form a ' nap-like' covering on portions of the dendrites of certain neurons. Although their significance is unknown, Cajal considered the spines to be dendritic devices for increasing surface area and rendering the synapse more intimate. In view of his opinion, it is interesting that the spines are most abundant on the Purkinje cell branchlets, a perfect site of'cruciform axo-dendritic connexions'."

Also on page 67 of Palay & Chan-Palay, they estimated that a 2 mm long parallel fiber would pass through the dendritic fan of 225 Purkinje cells. This value suggest the planes of adjacent Purkinje cells are nine microns apart. With a thickness of the dendritic tree frequently takes as nine microns, the Purkinje cells in the figures of **Section 10.2.4** are virtually touching each other. Fox & Barnard addressed this question of spacing in the body of their paper.

Fox & Barnard provided a very valuable paper, even though it used the technology available in their time. They did use oil-immersion objectives in their light microscopy. They noted,

> "Why thousands of fibres are in touch with a Purkinje cell's terminal spiny branchlets is unknown, but it may be meaningful in the light of the recent disclosure that dendrites have properties different from those of the cell bodies and axons. Clare & Bishop (1955 a, b), studying intercortical paths activating only the apical dendrites of the cortical pyramids, have obtained evidence indicating that dendrites in the cerebral cortex do not behave as all-or-nothing conductors. Repetitive stimulation maintains them in a persistent state of negativity. They have no absolutely refractory period, and the duration of their response is much longer than that of the cell bodies and axons. They modulate the activity produced in cell bodies by afferent stimulation of cell bodies and they are capable of sustaining local activity at a stimulated region without propagating impulses to the cell body or axon. Interestingly, these disclosures were made in paths synapsing like the parallel fibres on Purkinje cell branchlets-both are exclusively axodendritic and both end on terminal spiny branchlets."

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[74]Fox, C. & Barnard, J. (1957) A quantitative study of the Purkinje cell dendritic branchlets and their relationship to afferent fibres *J Anat* (Lond.) Vol 91, pp 299-313

The above paragraph is critical substantiation of the Electrolytic Theory of the Neuron and particularly how the stage 3A encoding neurons operate, with the dendrite essentially operating in the analog mode while the axon operates in the pulse mode, with the two coupled by feedback through the podite (or base) lead of the neuron (**Section 9.1.1.6** and **Section 7.3.4 of PBH**).

Fox & Barnard go on,

> "Is the fantastic number of parallel fibres on Purkinje cell branchlets responsible for the fast activity of the cerebellar cortex? Adrian (1935) and Dow (1938) have shown that the electrical discharge frequency of the cerebellar cortex is one of the fastest in the central nervous system. Snider & Eldred (1948), by isolation experiments, demonstrated that this rapid activity results from intrinsic rather than extrinsic mechanisms. Brookhart, Moruzzi & Snider (1951), with microelectrode recordings of unit activity, have found this activity to originate from structures in the Purkinje cell and/or granule cell layers. If, for the moment, this activity is speculatively assigned to the Purkinje cells, say as a result of their rich connexions with parallel fibres, the silence Brookhart et al. encountered in the molecular layer, while probing with microelectrodes for unit spike activity, may be explained by the dendritic properties Clare Bishop disclosed."

### 17.5.1.4 Interpreting the papers of Ito extending into the 1980's

Ito, a member of the Eccles team earlier, published a major text on the cerebellum in 1984. While considerably more advanced than the Eccles, Ito & Szentágothai text of 1967, it is currently more an archive of data than a depository of knowledge. The discussions and assertions are archaic in the presence of the three-terminal neuron and the Electrolytic Theory of the Neuron.

Ito developed his approach to analyzing the role of the cerebellum in his General Introduction. He defines a very high level "Constructive Approach" to replace the earlier, and widely used, "Expeimental Approach." The problem is that the constructive approach is entirely dependent on the molecular processes within and associated with the neuron. His unstated constructive approach is based on the concept of the chemical neuron rather than The Electrolytic Theory of the Neuron. He did not discuss the foundation for his constructive approach. The constructive approach has not moved forward since 1984.

Prior to developing his constructive approach to analyzing the operations of the cerebellum, Ito asked three basic questions concerning the cerebellum,

1. How is the cerebellum constructed (its structure)?
2. How does the cerebellar circuitry operate(its circuitry operations)?
3. What does the cerebellum do (its functional role)?

These are clearly fundamental questions concerning virtually any "machine." Ito notes the similarity of his three quiestions to those of Marr (1982), who stated his three questions in the reverse order to that of Ito. Ito asserts his three questions are independent and need to be addressed individually. In mathematics, three independent questions are in fact orthogonal and their order of presentation is of no value.

Ito does not address these questions in what would today be considered necessary rigor. In fact, his description of how the cerebellum operates is at best conceptual. He does not describe the cerebellar circuitry at any fundamental level. His description of the cerebellar circuitry remains conceptual.

This chapter will provide much more information in response to these questions than did Ito.

## 17.6 Block diagrams, schematics and circuits of memory & learning EMPTY

[xxx very little information concerning the operations of the granule cells, basket cells and Golgi cells ]

**This Section 17.6 and Section 17.5 will closely track and exchange material with Section 15.8.8 in "Processes in Biological Vision," the Project "Vision" on the ResearchGate.net site.**

## 17.6.1 Diagrams related to the cerebellum

Most of the recent figures in the academic literature relating to the cerebellum originated as pedagogical tools. Schematic diagrams related to the cerebellum, and based primarily on morphology, are described in detail in the lecture series from the Univ. of Wisconsin–Madison[75] (**Section 10.2.4** and **Section 10.2.5**). Much of that lecture material was drawn from the exploratory research material presented in this section. Schematics of the cerebellum, and obtained primarily from electrophysiology are the focus of this major section.

The earliest work on the electrophysiology of the Purkinje neuron was by Granit & Phillips in 1956 (See **Section 2.10.3**). As noted in **Section 17.6.1.2**, Eccles et al. (1967) have provided the most electrophysiological data relating to the cerebellum found in the literature. Recently, Wright (2016) has provided additional details related to the Purkinje neuron in the context of the cerebellum (**Section 17.6.1.4**). The work of Wright suggested to this investigator that the Purkinje neuron may be the major memory storage element accessed and controlled by a supporting parallel fiber "switch" similar to a man made switch used in telephony. This more complex switching engine (consisting of the circuits of the cerebellum and the "interposed nuclei," found within the white matter of the cerebellum) appears capable of supporting many functions related to the creation, storage recall and update of memories.

This section is complimentary to the morphology in **Section 10.2.4**. There are a variety of circuit diagrams related to the cerebellum in the literature and on the internet. They are generally inconsistent, avoid describing the source and target of the signals passing through these circuits. do no show the character and polarity of intermediate signals, and are invariably based on the chemical theory of the neuron[76,77]. They do not demonstrate how memories are acquired, maintained or updated within the cerebellum.

### 17.6.1.1 Cell level diagrams of the Purkinje cell of Granit & Phillips

[xxx See **Section 2.10.3** ]
Granit & Phillips (1956) provided considerable detailed information concerning the Purkinje neuron using the crude test instrumentation of their day. This material has been used to develop a "Mark 1" interpretation of the Purkinje neuron presented in **Section 2.10.3**. The Mark 1 is compatible with all of the aspects of the three terminal neuron based on the Electrolytic Theory of the Neuron presented in this work.

> The use of the label, "giant spikes" by Granit & Phillips is a bit inappropriate. Only positive going giant spikes of approximately 1.0-1.5 msec duration qualify as action potentials. They are typically 55 to 110 mV in amplitude depending on the biasing of the source relaxation oscillator. Giant spikes that are negative going actually represent the monopulse waveforms created internally within the base or poditic plasma. They are typically less than 33 mV in amplitude.

Based on the Mark 1 Purkinje neuron of **Section 2.10.3**, much of the material in the 1956 material can be reinterpreted on a firm foundation.

In their figure 7, the waveforms are clearly negative going pulses from a quiescent level of –20 mV from the ground point assumed to be the adjacent matrix. The pulses are nominally 30 mV high and negative going. These pulses clearly originate in the poditic terminal of the Activa. At their peak they correspond to the point of saturation in the collector to base potential of the Activa (saturation potential of 17.5 mV). Simultaneously, the collector circuit has created a positive going action potential of nominally 55 mV.

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[75] Neuroanatomy Dept. (as of 2005) Cerebellum (page 537). Univ. of Wisconsin–Madison http://www.neuroanatomy.wisc.edu/coursebook/cerebellum04.pdf

[76] Neuroanatomy Dept. (as of 2005) Cerebellum. Univ. of Wisconsin–Madison http://www.neuroanatomy.wisc.edu/cere/text/r3/cr.htm#circuit

[77] The Neurotransporter Group (as of 2017) The Cerebellar Cortex. https://neurotransporter.org/Cerebellum.html

As developed in **Section 9.xxx**, by properly biasing the Activa within a neuron, the Activa can be converted into a monopolar monopulse oscillator that employs positive internal feedback (no feedback path external to the neuron required). This positive internal feedback generates both the rising and falling phases of an action potential. There is no requirement for a separate "inactivation" mechanism or cathodal mechanism as introduced by Frankenhaeuser in 1952. The discussion on page 532 relative to potential inactivation mechanisms is not necessary. The statement on page 533, "A synaptic [feedback] loop through the basket cells which are large cells, in size second only to the Purkinje cells, should be given first rank in a list of possible working hypotheses." is also unnecessary.

Their figure 8 shows a variety of interesting waveforms. Figure 8(2) clearly shows the d.c. record resulting from the probe penetrating the axolemma. The waveform shows two low amplitude sinusoids superimposed on a slowly rising ramp, apparently applied to the dendritic terminal initially and resulting from class B amplification. The third sinusoid on the ramp crosses the threshold level for monopulse generation in the axon circuit resulting in one positive going action potential. The sinusoids are labeled positive-going prepotentials in their paper.

Page 534 describes the limitation on the rate at which action potentials can be generated by their Purkinje neuron due to the refractory period generated by the exponential decay waveforms in the dendroplasm and podaplasm circuits. They note a maximum reliable rate of about 200 cycles/sec. The net decay characteristic is shown in the inset at the upper right in figure 9. The fact that higher amplitude stimulation of the dendroplasm leads to higher sustainable pulse rates is compatible with the neuron based on the Serape representation.

## 17.6.1.1.1 The D-Potential of Granit & Phillips–a stage 3B output signal

Granit & Phillips identified a distinct waveform in the cerebellum of cats that they report in their 1956 paper (page 540). **Figure 17.6.1-1** reproduces their figure 13(1). Their text suggests the waveforms were obtained from penetration of a dendrolemma. The waveforms are clear examples of a stage 3B integrating neuron responding to 3 or 2 action potentials. In that case, the capacitance of the probe may have shortened the time constant of the dendritic circuit resulting in more prominent saw-toothing than would be expected of a good quality stage 3B integrating circuit. **Section 14.3.2.2** in **PBV** develops very similar waveforms in the stage 3B of any stage 3 propagating neural circuit. [xxx probably need to include in Chap 9 of this work ]

Granit & Phillips note the waveforms were always positive going unless the probe was pushed deeper into the cell where the polarity became reversed. This would be expected when the probe penetrated the podalemma.

In both cases, the amplitude of the integrated signal remains subthreshold. They note with respect to these waveforms, "Its curious discreteness and the large size, maximum 20 mV with *external* approach, lend support to our final standpoint that the D-potential is a response type in its own right belonging to dendrites or Golgi II cells." The interpretation here is they represent the integrated waveform from a parallel fiber (axon) originating as the axon of a granule neuron. The waveforms are generated in the cruciform junction between the parallel fibers and the dendritic tree. They are individually subthreshold but when combined with a signal from a climbing fiber, they reach the Purkinje neuron threshold for action potential generation.

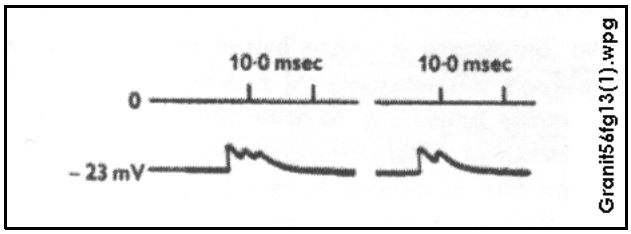


**Figure 17.6.1-1** A stage 3B integrating action potential decoder of Granit & Phillips. Two examples starting from the same –23 mV baseline but with stimulating pulses of marginally different amplitudes. The waveforms may originate in the cruciform junctions between a parallel fiber (axon) and the outer extremities of the dendritic tree of a Purkinje neuron. See text. From Granit & Phillips, 1956.

A question remains, are two or more subthreshold waveforms required to combine with one signal from a climbing fiber to achieve threshold potential. ***The precise configuration of parallel fibers and climbing fibers required is critical to the understanding of a Purkinje neuron as a memory storage element.***

Within the cruciform junction, the synapse may be the major component of the stage 3b integrator, along with

a significant capacitance on the post synaptic (dendritic) side of the synapse.

### 17.6.1.2 Circuit level diagrams related to the cerebellum by Eccles et al.

To appreciate the task of building a circuit model of the neurons within one folium of the cerebellum, **Figure 17.6.1-2** can be used. This figure appears to be the basis of the figures in **Section 10.2.4** that were missing attribution.

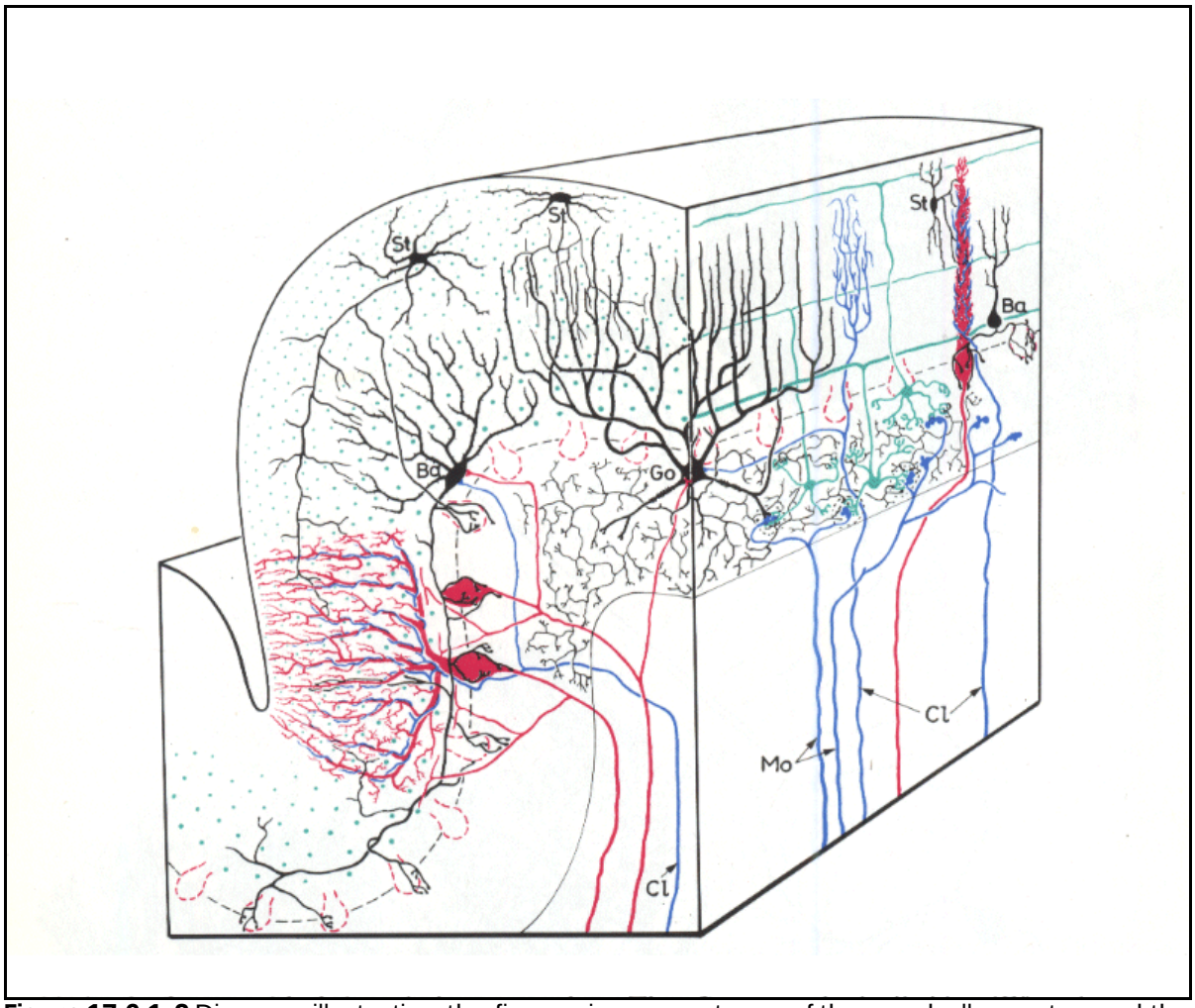


**Figure 17.6.1-2** Diagram illustrating the five main neuron types of the cerebellar cortex and the two kinds of afferents with their main interconnexions. "The afferents–both climbing, (Cl) and mossy, (Mo) fibers–are indicated in blue. The outlines of cerebellar glomeruli are drawn with black dotted lines. Granule neurons and parallel bibers in gree, Purkinje neurons and their axons in red, the three main kinds of interneurons: stellate cells (St), basket cells (Ba), and Golgi cells (Go) are shown in black." See text. From Eccles et al., 1967.

Based on the Electrolytic Theory of the Neuron (**Chapter 2**), a much more complete circuit diagram for a specific circuit within the cerebellum can be provided. [xxx provide a better circuit diagram ]

Eccles et al provided a text in 1967 focused on the circuitry surrounding the Purkinje neuron. It was supported by multiple papers published in 1966. Unfortunately, none of this material described the internal structure or operation of the Purkinje neuron. In many cases, their material reflects a pure empiricist, making measurements in the laboratory without having a null hypothesis about the character of the material he was

investigating. Some of their terminology is also unconventional. They describe the "invasion" of different morphological areas of the neuron by a conceptualized response to an antidromic stimulus. Figure 1 of the fifth paper (also slightly modified in fig 42B through 42J of Eccles et al., 1967) is a good example of their approach[78]. Chapter 5A(1) of the 1967 text should be discounted based on the discussion here. Without presenting any information about their concept of the internals of the neuron, they present a series of waveforms obtained from a deafferented Purkinje neuron stimulated antidromically, that is the axon was stimulated at a distance from the soma of the cell and data was collected from both the axon, via a separate microprobe, and the soma and dendritic structures based on their morphology. While the waveforms are consistent, their presentation, and accompanying discussion are not. Frames A through F are purported to be "spike potentials" recorded following stimulation by an unspecified waveform. From the imagery, the stimulus qualifies as an impulse (it being much narrower than the response within the axoplasm).

> With the stimulus qualifying as an impulse, the spike potential qualifies as the *impulse response* of the axoplasm and its containing lemma. Technically, it is not an action potential. Since the Activa remains cutoff, the impulse response is the characteristic of the axon (including its capacitive coupling to the dendritic and poditic plasmas) and its power supply. The power supply is described simplistically in **Section 2.10.3.1** by $V_{AA}$, $R_A$ and $C_A$. It is described in greater detail in **Section 2.3.2**.
>
> The previous paragraph speaks in terms of lumped constant parameters. At the size of the Purkinje neuron and its internal dependence on diffusion of electrical charge, a distributed parameter analysis is needed to account for the inflection in the rising phase of the impulse response noted by Eccles et al. using an arrow in figure 1.

These waveforms were matched to similar Frames G through K. The latter waveforms are quite complex and are plotted inverted relative to the potentials in the initial frames. In fact, the waveforms in the second group are the derivatives of the waveforms in the first group. These are precisely the waveforms expected of the Purkinje neuron based on the Electrolytic Theory of the Neuron. The Serape of the Purkinje neuron presented in **Section 2.10.3** and a more detailed discussion of the impedance related to the electrostenolytic axon of the generic neuron is shown in **Section 2.10.1.1**. In the case of the deafferented neuron with antidromic monophasic pulse stimulation of the axoplasm, the observed axoplasm waveform mimics the applied action potential–like stimulus. The "soma" waveforms in the second group actually represent the potential of the podoplasm in response to this stimulation under the conditions that the Activa is in the cutoff condition and the capacitance, $C_{AP}$ and the resistance of the poditic circuit, $R_P$ are in series. Under these conditions, the podaplasm waveforms should be the derivative of the axoplasm waveforms, based on the formulas of conventional electronics, $e_2 = (R_P \bullet C_{AP})(de_1/dt)$. Note the significantly smaller signal amplitude of the waveforms in frames G through K of figure 1 compared to frames A through F. The derivative of the impulse function is of higher amplitude than the derivative of the "spike potentials" because of its steeper leading and falling edges. The leading edges of the derivative of the impulse function are not shown explicitly.

Their designation IS–SD for the "initial axon segment"–"soma–dendritic membrane" should be *changed* to read the IS–SP, "initial axon segment"–"soma–podaplasm." The probe penetrating into the soma was actually in contact with the podaplasm enclosed by its lemma, a region usually described morphologically as the hillock of the neuron.

Figure 2 of the 1966e paper provides some excellent waveforms and time delays but the text requires extensive rewriting. The designation LOC → J.F. indicates the stimulation of the J.F. following a delay after the stimulation of the surface of the folium by a local electrode, LOC.

Their figure 13 of paper 1966e (and fig 46A–C in the 1967 text) attempts to describe the *invasion* of the neuron by an antidromic signal. Invasion is a questionable term in the case of the Purkinje neuron. As noted above, the appearance of a differentiated waveform in the podaplasm is by capacitive coupling, not by diffusion alone. A similar differentiated waveform is potentially generated in the dendroplasm of the neuron, but not measured in these experiments. Figure 13 (and fig 46A–C)along with the accompanying text can be

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[78]Eccles, J. Llinas, R. & Sasaki, K. (1966e) The action of antidromic impulses on the cerebellar Purkinje cells *J Physiol* vol 182, pp 316-345

disregarded in favor of a more detailed lump parameter analysis.

The Eccles and colleagues papers of 1966 contain a wealth of information. However, they require almost total reinterpretation in the context of the Electrolytic Theory of the Neuron. This time consuming processes will only be performed selectively below.

Eccles, Ito & Szentagothai have provided the most data defining the circuit operations of the neurons most associated with the Purkinje cells of the cerebellum[79]. Unfortunately, since Eccles et al. assumed these were all stage 3 pulse generating neurons, they primarily used impulse stimuli to evaluate these circuits. In case of the Purkinje cell, they did provide one figure 91(c)that clearly demonstrates its Class B analog operation. This figure will be discussed further below.

Eccles et al. used a relatively gross laboratory technique to collect their data. It was similar to that used by Granit & Phillips. Instead of dissecting the folium of the cerebellum to gain access to particular neurons of adjacent interneural areas, they chose to penetrate the pial surface of the folium to a specific depth and assume that depth placed their probe at a specific location in interneural space associated with a particular layer of the folium. They then made a number of assumptions relative to the collected data, frequently related to antidromic signals associated with the Purkinje cell axons or axoplasm. [xxx need figure here showing depth scale used ]

Eccles et al. expressed no knowledge of the internal workings of the Purkinje cell and other neurons of the cerebellum. From their discussions, it can be ascertained that they relied upon the two-terminal theory of the neuron based on chemical theory. This leaves them in a difficult position to explain some of their waveforms that exhibit unusually low voltage ranges and polarities. Thus, these waveforms must be carefully studied to reinterpret their source; relatively distant interneural locations, within or near the podaplasm of the cell or representative of the axoplasm o the cell.

Chapter I of Eccles et al. provide a wealth of detail concerning the histology of the folium and even suggest that the initial polar structure emanating from the base of the purkinje is not a fully formed axon, which only presents itself after an external narrowing at the point of myelination. ***This is a significant feature if confirmed***. It places any stage 3A encoding operation outside of the plasmas within the lemma of the Purkinje cell (potentially at a modified Node of Ranvier). It also suggests that the bulk of the Purkinje cell contains and distributes analog electrical signals (as will be asserted in this work after further analyses in this major section.

Eccles et al. describe the probe depths they used on pages 61-63. However, the description is cursory and refers the reader to an earlier work involving live cats[80]. **Figure 17.6.1-3** reproduces the figure from that work. Probe results from 700 microns are occasionally reported in this material. The caption for this figure reads,

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[79]Eccles, J. Ito, M. & Szentagothai, J. (1967) The Cerebellum as a Neuronal Machine. NY: Springer-Verlag *reprinted 2013*

[80]Eccles, J. Llinas, R. & Sasaki, K. (1966a) The inhibitory interneourones within the cerebellar cortex *Exp Brain Res* vol 1, pp 1–16

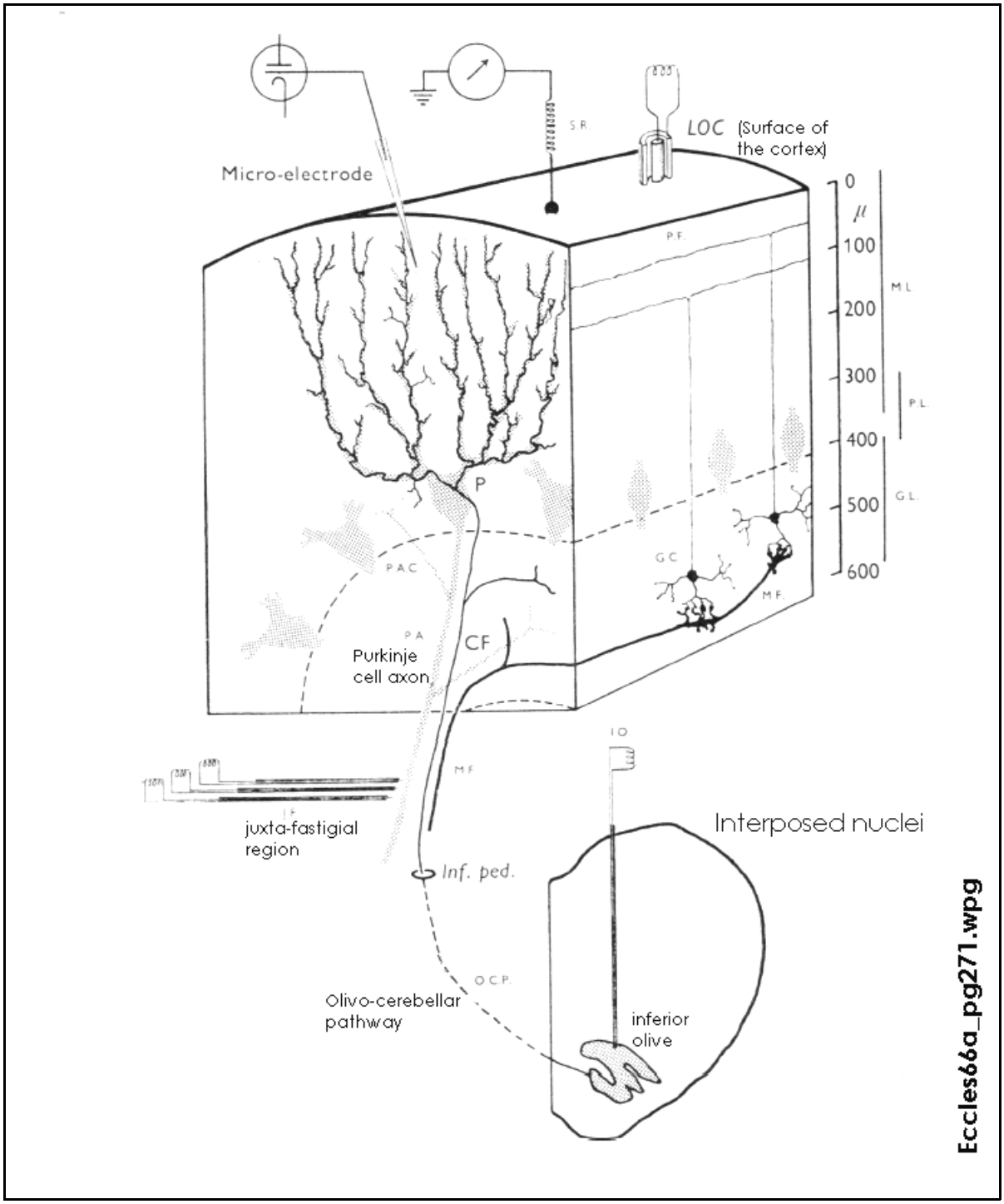


**Figure 17.6.1-3** The test protocol of Eccles, Llinas & Sasaki. The multiple horizontal lines at lower left indicate the potential for multiple stimuli of the extremity of the first axon segment of the Purkinje neuron. See text for long discussion. From Eccles, Llinas & Sasaki, 1966a.

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“Diagram of the experimental arrangement. A small portion of the cerebellar cortex with its three main layers, the molecular (M.L.) granular (G.L.) and Purkinje (P.L.) is schematically drawn, and their corresponding depths are marked in the right side of the figure. The two inputs are shown to the Purkinje cell (P): the climbing fibre (CF) with its extraordinarily extended synaptic contacts on the dendrites of the Purkinje cell; and the mossy fibre (M.F.), granulae cell (G.C.), parallel fibre (P.F.) pathway. The climbing fibres are the mode of termination of the olivo-cerebellar pathway (o.c.p). (see text) which arises in the contralateral inferior olive (i.o.) and reaches the cerebellar cortex through the ipsilateral inferior peduncle (inf. ped.). The Purkinje cell axon (P.A.)has collaterals (P.A.c.)which ramify in the granular and the molecular layer of the cortex forming the infra and supra ganglionic plexus respectively. Stimulating electrodes were located in the inferior olive (i.o.), juxta-fastigial region (J.F.) and the surface of the cortex (LOC). The recordings were made from the surface of the cortex with a ball electrode (S.R.) and in depth with micro-electrodes.”

The text referred to in the above quotation appears to be,

“On the general grounds of the widespread distribution of the olivo-cerebellar fibres Dow (1942) suggested that the climbing fibres originated in the inferior olive, all other cerebellar inputs being via mossy fibres. But it was not until the very careful degenerative study by Szentagothai & Rajkovits (1959), that a sound experimental basis was provided for the olivary origin of the climbing fibres, as illustrated.”

They then note in connection with the above figure, but on page 63 of Eccles et al.,

> “*Under present experimental conditions [1967 and earlier], the only criterion for discriminating between the three types of interneuronse is provided by the depth below the surface of the cortex at which the sharply localized spike potentials can be recorded, it being assumed that this gives the approximate level of the respective somata.*”

In the context of the Electrolytic Theory of the Neuron, large positive going pulse waveforms, greater than 10 mV, would be associated with the axoplasm of a stage 3 neuron. Small negative going waveforms, analog or pulse, would be associated with the podaplasm (largely within the somata). Small positive going waveforms, analog or pulse, would be associated with the dendroplasm (largely within the somata).

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Figure 91( c) of Eccles et al. is reproduced here as **Figure 17.6.1-4**. It exhibits a number of significant features. The minor spike at lower left appears to indicate the time the stimulus was delivered to, not from, the J.F. Assuming the leading edge of the first major spike occurs 5 msec after the timing spike, it is likely that most of this delay occurred within the dendritic tree of the Purkinje cell (from the location of synapse #1 (in **Figure 17.6.2-1)**. The height of the first pulse exceeds +68 mV. Any waveform exceeding +20 mV in amplitude must be generated in the axoplasm of an *in vivo* neuron. Furthermore, any waveform in the axoplasm exceeding 5 mV in amplitude in an *in vivo* neuron cannot be considered subthreshold. The amplitude of this pulse suggests the neuron is operating in the Class B linear mode. The subsequent amplitudes of the pulses serves to confirm this analog operating mode. Otherwise, the pulses would all be of equal height. The unequal spacing between the subsequent peaks suggest the first peak occurs due to the signal crossing the closest synapse (#1synapse)) to the soma of the Purkinje cell. Subsequent peaks would reflect the additional distance traveled by the signal along the climbing fiber axon and the dendritic structure of the Purkinje cell before participating in a synapse, #2 and higher. The variation in the amplitude of the subsequent peaks would be indicative of the dimensions of the synapse involved.

***These conditions are very strong evidence that this Purkinje cell was operating in an analog mode.***

Contrary to assertion #2 of their Summary, the 5-7 msec sequence is clearly not of "all-or-nothing character." It is also clear that this waveform does not lose amplitude with time due to fatigue or loss of necessary chemical constituents. Fig. 4 of the 1966a paper shows additional waveforms like figure 91( c). It is not clear why they assert variable height peaks in their waveforms are "all-or-nothing in character." Later in the 1966a paper, they discuss the complications encountered since they did not record the actual stimulus delivered to the Purkinje cell by the presumed direct climbing fiber (axon) from the inferior olive cell(s).

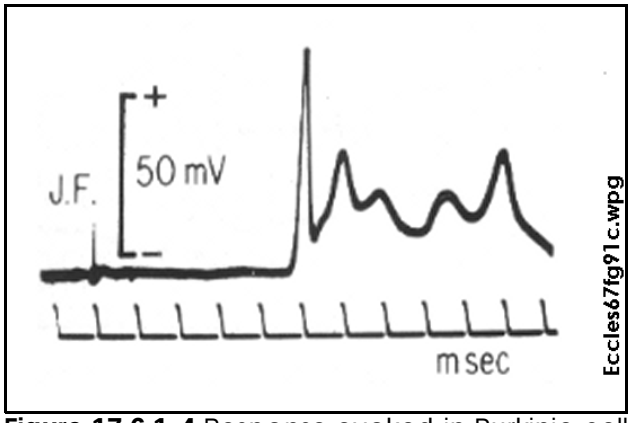


**Figure 17.6.1-4** Response evoked in Purkinje cell of cat by climbing fiber impulses activated from the inferior olive and juxta-fastigial stimulation, J.F. The original caption indicated the stimulus strength was subthreshold. However, the magnitude of the waveform suggests otherwise. See text. From Eccles et al., 1967.

Comment #9 in their summary hints that they were performing a variant of the patch-clamp procedure in 1967. However, there was no suggestion they were introducing dye through their electrical probe to localize their precise source of data at a later time. There is no indication they electrically compensated their electrical probe to avoid test-set evoked under or over shoot in their waveform recordings.

There is considerable data in the 1966a paper that can be re-interpreted using "the Electrolytic Theory of the Neuron" and considering the travel times involved in the length of the dendritic paths relating to the Purkinje cells. That theory demonstrates that antidromic signaling is not practical from the post synaptic to presynaptic portions of a synapse or from the axoplasm to the dendroplasm of an individual neuron. The discussion concluding the paper is far ranging and worthy of careful reinterpretation based on the current (2017) database related to the performance of the Purkinje cell.

Ito (page 37, frame D) provides a waveform from a Purkinje axon collateral that appears to be a single positive going response that is 10 msec wide[81]. He does not describe the stimulus that causes this response. It may have been a pulse of finite width. [xxx get paper and interpret ]

[81]McCrea, R. Bishop, G. & Kitai, S. (1976) Intracellular staining of Purkinje cells and their axons with horseradish peroxidase *Brain Res* vol 118, pp 132-136

[xxx continue here after copying pages of chapter IV of 1967 book ]

## 17.6.1.2.1 Additional features of the Purkinje cell

According to Eccles et al. (1967, page 9), "The axon of the Purkinje cell originates from its lower pole and gradually becomes thinner over the first 30 microns or so. Then quite abruptly its diameter increases (their figure 4C) to the normal thickness and it becomes myelinated. . . . The collaterals are myelinated . . ."

## 17.6.1.2.2 Additional features of the indexing associated with the Purkinje cell

Eccles et al. illustrated an additional feature that appears to be associated with the indexing of the Purkinje neurons, **Figure 17.6.1-5**. It is attributed to Szentagothai[82].

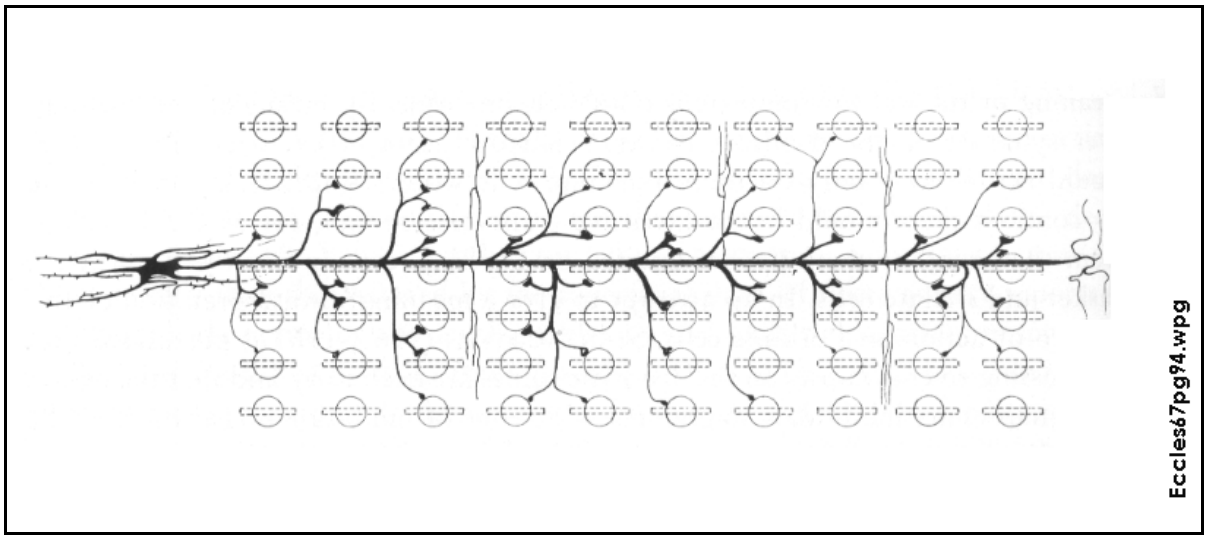


**Figure 17.6.1-5** Matrix of Purkinje cells accesses by a basket cell. The Purkinje cells are indicated by circles and overlying bar as if viewed from above—potentially reached by the descending branches of single basket axon. The basket cell is seen at left. The longitudinal axis of the folium is vertical in this figure. From Szentagothai, 1965a.

The accompanying text in Eccles et al. is quite useful. Regarding the axon collaterals of the basket cells they noted, "According to Fox and Barnard (1957), they can be traced as far as the 18th Purkinje cell in the monkey. Our own observation on the cat have been based both on Golgi pictures and on degeneration studies either on isolate folia or after a longitudinal cut through the entire depth of the molecular layer, and have give a rather smaller distance to about 10 Purkinje cells." They also note from the observations of Estable (1923), the descending ranches of the basket axons also spread at right angle to the transverse plane, that is along the folium. The transverse spread of basket axon collaterals is thought by Fox to reach as far as six Purkinje cells in both directions, so giving a distribution to twelve cells, which would meant hat a single basket axon could contact as many as 12 x 18 = 216 Purkinje cells." They suggest their calculations would suggest a more conservative 70 Purkinje cells. Before proceeding to a broader discussion, they note, "*The Purkinje cell baskets are a synaptic system of almost unique architectural design*." Emphasis added. They go on (page 95), " xxx

## 17.6.1.2.3 Parametric (abnormal) excitation of the Purkinje neurons

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[82]Sentagothai, J. (1965a) The use of degeneration methods in the investigation of short neuronal connexions *In* Singer, M. & Schade, J. *ed*. Progress in Brain Research, vol. 14, pp 1-32 NY: Elsevier

Eccles et al. allocated many pages of Chapters 5 & 6 to the excitation of Purkinje neurons by highly un-natural (parametric) means. They cited Eccles, Llinas & Sasaki (1966e) as their source. The waveforms recorded and the resulting data may be of low scientific value, but they may provide some additional understanding of the potential operation of the Purkinje related neural circuits.

In general, they provided,
• external surface impulse excitation (their label LOC) to the surface of a folium with the intent of stimulating underlying parallel fibers
• *antidromic* excitation of the outer extreme of the initial axon segment of the Purkinje neuron via their juxta-fastigal (their label J.F.) excitation, by stimulating the tissue adjacent to the fastigial nucleus of the interposed nuclei.

and recorded intracellular signals from,
• the same initial axon segment but from a location nearer to the soma of the Purkinje neuron.

The signals recorded and discussed appear on pages 83–92 & 99-105.

> Much of the material on the above pages can be interpreted differently under the Electrolytic Theory of the Neuron compared to the archaic chemical theory. The chemical theory assumes a one chamber neuron compared to the three-chambers identified in the Electrolytic Theory; the dendritic, poditic and axonal chambers where each is enclosed by a separate lemma. The chemical theory also depends on the diffusion of ions through a fluid medium within the outer lemma. Alternately, the Electrolytic Theory asserts the material within each chamber is in the liquid-crystalline state and all charge transport is by semiconductor mechanisms. These mechanisms support the actual charge velocities measured within neurons; these charge velocities are not compatible with conventional ionic velocities within fluids. Eccles et al. describe a "slow wave" with a velocity of 0.4 m/sec (16 inches/sec); this is very fast for ionic transport in a liquid (absent stirring) and more appropriate for charge transport in a semiconductor. The conventional ionic velocities are implied but not asserted in the cross-sectional views of neurons in their figures 46 & 63. ***With these alternate interpretations, the cross-sectional views presented in the next section become much more realistic***. Sections C & D of their chapter VI can be largely dismissed as archaic.

A feature of figures 52(G) and 53(B) is the likelihood that the recorded intracellular waveform recorded at the initial axon segment close to the soma is extended to over 50 msec by integration of the pulses (if any) generated and propagated from within the parallel fibers. Such an integration of these pulses could support the earlier suggestion in this work that the cruciform connexions between the parallel fibers and the Purkinje dendritic tree consists of a glomeruli where the synapse qualifies as a stage 3B action potential train decoder (**Section 9.7**). This would entail the presence of a significant capacitance within the glomeruli. Two major question arise. First is relative to the low amplitude of the recorded waveforms. They appear to all be in the few mV range, that is not indicative of an action potential associated with normal, orthodromic neuron analog or pulse output signal production. Second, the lack of any serration associated with their long pulse waveforms, and anticipated if the waveforms arose from stage 3B pulse integration or from the summation of the staggered pulses (their volley) associated with a fascicle of parallel fibers. They defined a "P-wave that was produced by the conditioning parallel fiber volley as in frames C to F of figure 52." The P-wave is shown to have a width of near 10 msec at its maximum width. This is considerably narrower than the time course of the antidromic spike potential in the cerebellar cortex presumed to be generated by the parallel fiber volley resulting from LOC stimulation. There is also the question of how to interpret the other frames in figures 52 and 53 also generated by the LOC stimulation followed by J.F. stimulation. Many of these waveforms appear to be the differentiated form of some stimulus narrower than, but similar to, the P-wave. Their amplitudes were also in the few mV range that might be reasonable for the derivative of a higher amplitude output signal. The potentially differentiated waveforms were recorded at a depth of 500 microns and without verification that they were the result of intracellular electrical probing.

The data in 1966e is clearly exploratory in character; no circuit diagram was provided to support the discussion. The 1966e paper shows a variety of waveforms that are clearly differentiated versions of the impulse response of the actual pulse encountered. Such an impulse response clearly defines the circuit elements used to produce that waveform. In many cases, they used two impulses separated in time by 5 msec to stimulate antidromically their initial axon segment. The results of this volley (a J.F. followed by another J.F.) produced two differentiated impulse responses.

Figure 2 (A–D) may show a summation of a P-wave and a complex waveform resulting from the J.F. stimulation. Figure 2(B) could suggest indexing by the P-wave of information represented by the complex waveform. Figure 3(A) shows the origin of a complex wave at 800 microns likely due to a differentiation of the small amplitude impulse response waveform recorded at lesser depths.

Figure 10 shows significant degrees of differentiation of various numbers of pulses in repetitive J.F. stimulation recorded at a depth of 500 microns. The stimulating impulse rate was 310 pulses/sec. The pulse amplitudes are very small and the undershoots are about 30% of the height of the negative going 1 mV or less pulses.

### 17.6.1.3 What is the generic form of the Purkinje neuron?

There are at least three versions of the basic Purkinje neuron in the recent literature; Granit & Phillips of 1956, Eccles et al of 1967 and Altman of 1972. While several of these representations are based on Cajol, each is represented primarily in text form and based on small laboratory animal and individual cell sample sizes. **Figure 17.6.1-6** addresses these forms. The first is the coke bottle shaped form of xxx, with the fully formed axon emanating from the center of the flat bottom of the larger bulge in the shape of the bottle. The second involves a similar bottle shape but with a structure exiting from the center of the flat bottom of the larger bulge that is less than recognizable. Eccles et al. (1967) has labeled this structure a pre-axon (page 11). Here, it will be considered a portion of the Activa base structure (the podaplasm and poditic or inverting terminal of the neuron) terminating at the collector of the Activa (the axoplasm). This is in agreement with the observations of Eccles et al. based on electron microscopy.

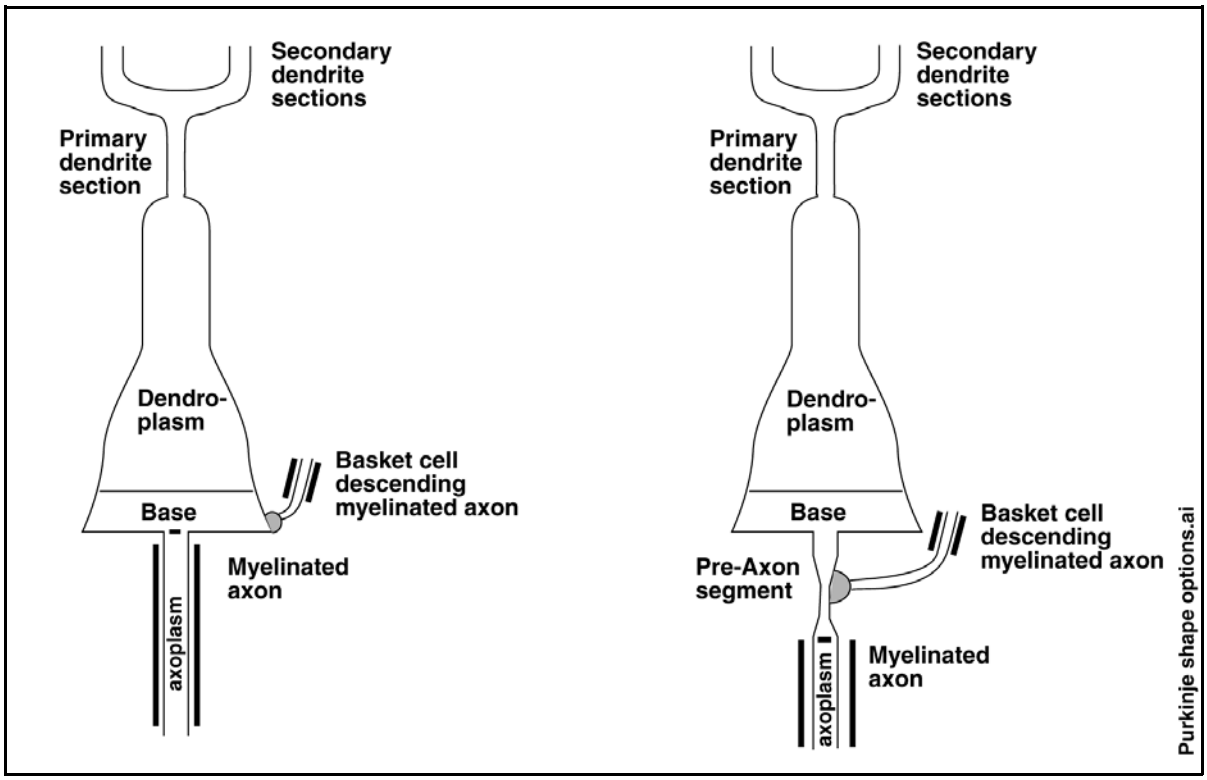


**Figure 17.6.1-6** Potential histological forms of Purkinje neurons. Left, the simplest variant proposed for the Purkinje neuron. The primary and secondary dendrites are isolated from the matrix by Bergmann cells. The descending axons of basket cells synapse with the perimeter of the base of the neuron, resulting in a inverting (inhibiting) input to the Activa. Right, the next most complicated variant. The primary and secondary dendrites are also isolated from the matrix by Bergmann cells. However, the descending axons of basket cells synapse with the protruding portion of the base, labeled the pre-axon by Eccles et al. in 1967.

In the form on the left, several texts have described the descending axon(s) of basket cells, although primarily

contacting the non-inverting dendritic tree of the Purkinje neuron, occasionally contacting the periphery of the base of the neuron in the area normally associated with the signal inverting poditic terminal. In the right frame, the descending axon(s) of basket cells, are shown as contacting the pre-axon area of the neurn. In both cases, the descending axon of the basket cell would be considered to be contacting the poditic (base) terminal of the Activa of the Purkinje neuron. However, in the second case, the poditic lemma of the neuron extends down to the end of the thin portion of the emanating structure to the point where the axolemma completes the formation of the Activa. At this point, the axolemma subsequently becomes myelinated and the signal transitions into the propagation mode of transmission.

In both cases, the descending basket axon synapses with the poditic terminal of the purkinje neuron (figure 56 in Eccles et al.)..

Altman (**Section 10.2.4.3.1**) contributed the third potential version of the Purkinje neuron when he reported a general myelination of the soma itself along with the primary segment, and possibly higher segments, of the dendritic tree(s) of the neuron. This assertion could be applicable to both of the earlier potential Purkinje neuron configurations.

Wright (2016) contributed to the potential forms of the Purkinje neuron, but only peripherally. He described the input of signals into the bottle shaped Purkinje neuron as discussed below from a block diagram. His diagram showed a number of axons synapsing with the lower body of his bottle without discussing the merits or purpose of these synapses. Here, these synapses are considered as contacting the inverting inputs of the differential input structure of the neuron.

### 17.6.1.4 5 Purkinje neuron action potentials from Rapp et al. 1994

Rapp et al. provided extensive discussion of the performance of the Purkinje neuron[83]. The data included extensive graphics showing the action potential patterns from cerebellar slices of the Purkinje of a guinea-pig. **Figure 17.6.1-7** reproduces their figure 1.

[83]Rapp, M. Segev, I. & Yarom, Y. (1994) Physiology, morphology and detailed passive models of guinea-pig cerebellar Purkinje cells *J Physiology* vol 474.1, MS 1737, pp 101-111

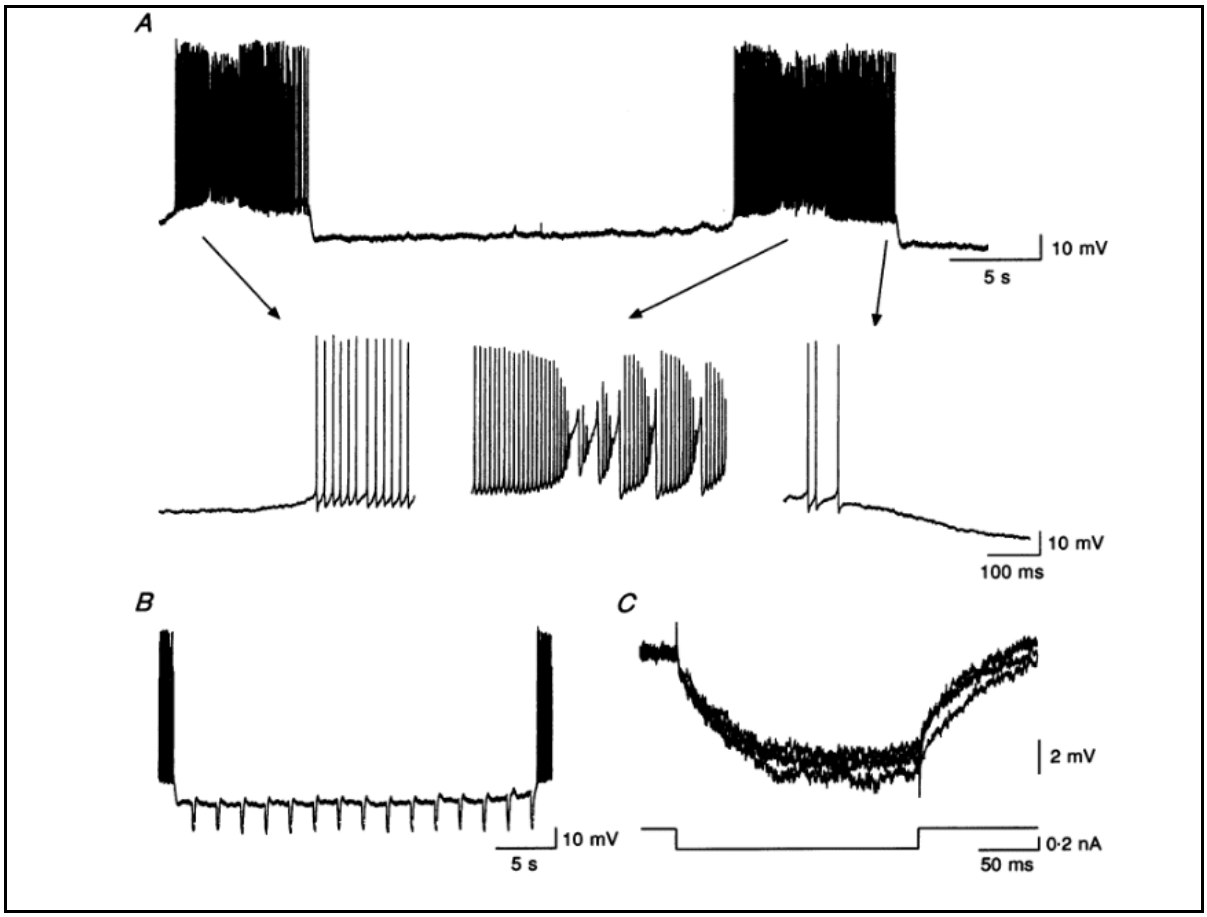


**Figure 17.6.1-7** Purkinje cell natural AP generation and response to parametric stimulation from cerebellar slices from guinea pig. See text for significant discussion. From Rapp et al, 1994.

The investigators performing the work were schooled in the chemical theory of the neuron and the caption to the figure demonstrated that background. The references to $Na^+$ and $Ca^{2+}$

> "Measuring ~~cable characteristics~~ [performance] of Purkinje cells [as class B amplifiers] during the interburst quiescent phase A, intracellular recording from a spontaneously bursting PC. The firing pattern during a burst is shown at an extended time scale in the lower traces. Each burst starts with high frequency fast ~~(Na+)~~ spikes (left arrow), followed by several smaller and broader ~~$Ca^{2+}$~~ spikes (middle arrow). The burst ends with a prolonged hyperpolarization as shown by the right arrow. B, voltage responses (shown as small negative deflections) to successive constant hyperpolarizing current pulses delivered via the recording electrode during the interburst phase. C, superposition of the first three voltage responses shown in B at a faster recording rate. The similarity between these traces indicates that during this time window the membrane properties changed only slightly."

The recorded spontaneous waveforms of frame A show full amplitude monopulses of 60 mV based on the pulse patterns in B below the left and right arrows. The waveforms in the middle of the figure on an expanded database do not appear to be an actual expansion of the recording of the specific pulse group on the right in frame A. The maximum pulse height is different and the individual pulse groups exhibit significant fatigue due to inadequacies in the electrostenolytic power source with a time constant on the order of 50 msec. The two pulse groups in frame A show some instability in the electrostenolytic power supply (ripples along the top and bottom edges of the pulse groups) but not of the magnitude of the pulse groups below the middle arrow. The full height waveforms shown in the middle row show signs of inadequate electrical compensation in the test probe (some uncompensated shunt capacitive loading by the probe itself. The ramp to the left of the left pulse group and to the right of the right group, as well as the ramp between the pulse groups, would suggest

the axoplasm has a quiescent operating potential of about 142 mV. There is a suggestion that the Activa within the Purkinje neuron is biased so that the emitter associated with the non-inverting dendritic input is near a threshold of about 40 mV versus the base associated with the inverting poditic input. This may be important when discussing how the indexing signals are applied to the Purkinje neuron acting as a fundamental memory unit.

Frame B is quite informative. As indicated in the original caption, the two monopulse action potential groups were spontaneous. They are of consistent height and very similar to those shown in frame A. The waveforms in between the pulse groups are due to the test set parametrically stimulating the axoplasm during the interval when the emitter to base potential of the Activa within the neuron is biased below threshold but above cutoff (class B operation). As a result, the response to the hyperpolarizing current pulse shown is stimulating the axoplasm of the Activa while the collector current passing through the collector to the base of the Activa appears as an impedance larger than that of the electrostenolytic power supply. The waveforms in C, both during and after the pulse exhibit similar time constants of about 50 msec for the power supply. This time constant would apply to the total capacitance of the axolemma and test probe capacitance multiplied by the output resistance of the electrostenolytic power source. The voltage amplitude of these transients are about 6 mV and both show noise on the waveform. A signal of this amplitude is not sufficient to drive the Activa into a suprathreshold condition due to axoplasm to podaplasm capacitive coupling. The very narrow spikes at the inflection points of the two transients is probably due to the switching within the test equipment. The 6 mV amplitude of the transient shown in frame C does not agree well with the 13 mV transient in frame B. Here again it appears the waveforms shown are not necessarily from the same recording or there is some loss in fidelity in the voltage scales shown.

The pulse groups in frame A show minimal presence of any encoded analog information. The expanded waveforms shown on the left and right of the middle line both show one missing pulse. These could be the result of encoding driven by a preceding neuron but this appears unlikely in a cerebellar slice *in-vitro*.

There is additional information to be extracted from the other figures of the Rapp et al. paper based on the Electrolytic Theory of the Neuron. Figure 2A for instance shows a sufficiently different set of waveforms to suggest a change in the order of the differential equation describing the operation with and without the presence of cesium ions. Their discussion of the “underdetermined” character of their extensive model of a Purkinje neuron with its dendritic tree is very interesting. Underdetermined is a term of art among circuit analysts and designers. They describe their model as “passive” even though the generation of action potentials strongly implies an active element somewhere in their Purkinje neuron. They did not provide a schematic of the internal elements or the external elements of their model. Because of this situation, they speak of anomalous rectification and “Because of the instability of the membrane potential, the neuronal properties have to be characterized at a given membrane potential.” etc. While they speak of, and entitle their paper, cable properties of the axon, they do not address a myelinated axon segment (or any Node of Ranvier) that characterize the actual cable properties associated with the axon of a Purkinje neuron.

### 17.6.1.5 Expansion of the concept of the Purkinje cell from Wright, 2016

Wright conceived of a gross morphological model of the Purkinje neuron, **Figure 17.6.1-8**, that can be further expanded to account for more of the functional features observed in the Purkinje cell and its adjacent circuits.

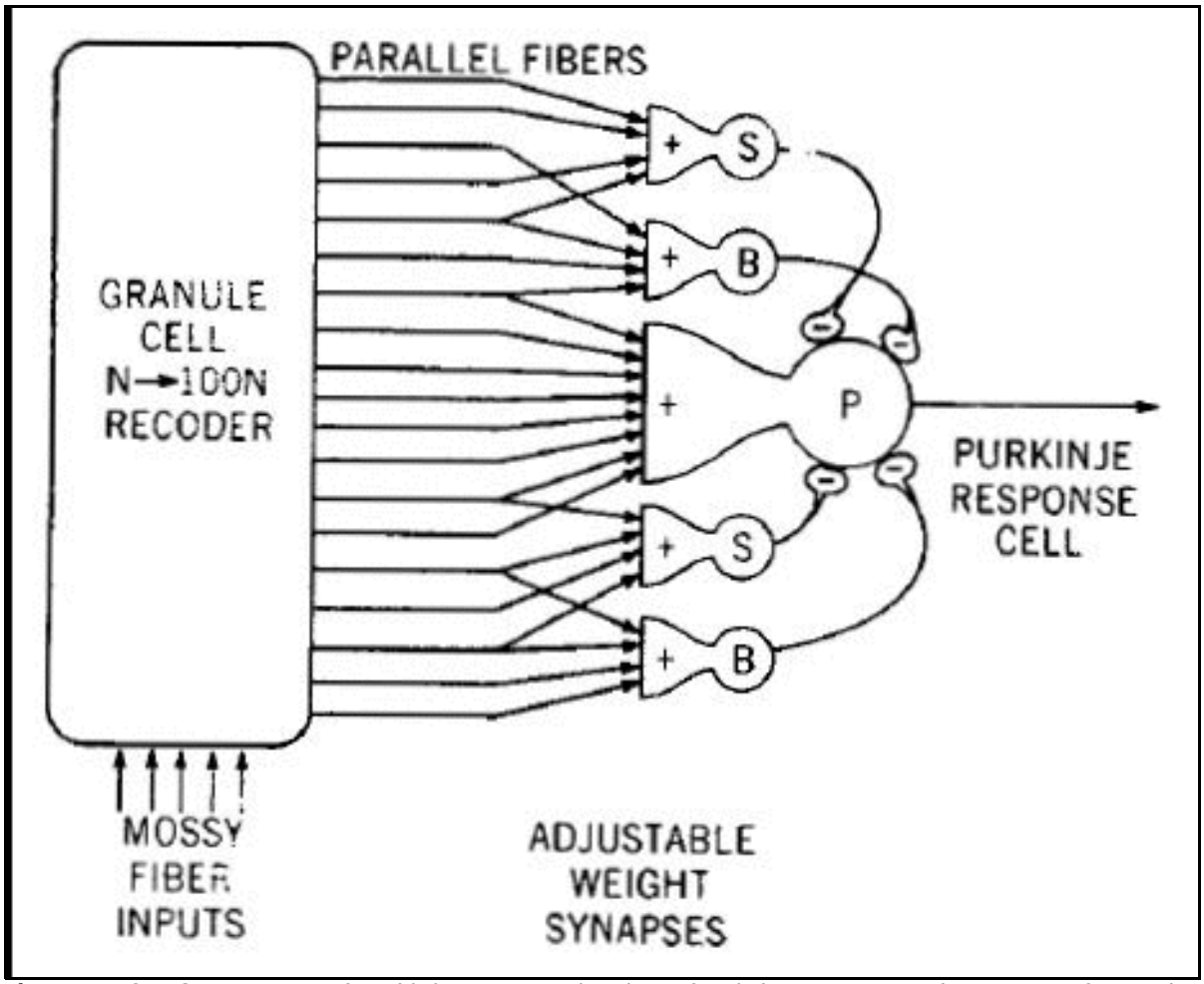


**Figure 17.6.1-8** Concept of Purkinje neuron circuitry of Wright, 2016 ADD The range of recoder granule cells, the routing of parallel fibers & the routing of axons to the lower soma of the Purkinje cell are apparently for illustration only. See text.

**Figure 17.6.1-9** provides an alternate representation of the Purkinje memory cell based on its differential input and pre-axon output. The amplifier shown is actually a stage 3A encoder. It essentially forms a first Node of Ranvier. **Section 17.7.6** will expand on this representation.

Eccles et al. have addressed the input structure at upper left in several different sections of their book. The most common representation is that of a climbing fiber synapsing multiple times with a single dendritic branchlet. This structure may be repeated hundreds to thousands of times along the branchlet. Eccles et al. have described the pre-axon on their page 11, the associated stellate and basket cells on pag 15 & 17, the Golgi vs Large stellate on page 22 and the Golgi vs fusiform cells on page 27.. They have also described potential learning options on pages 34 & 35.

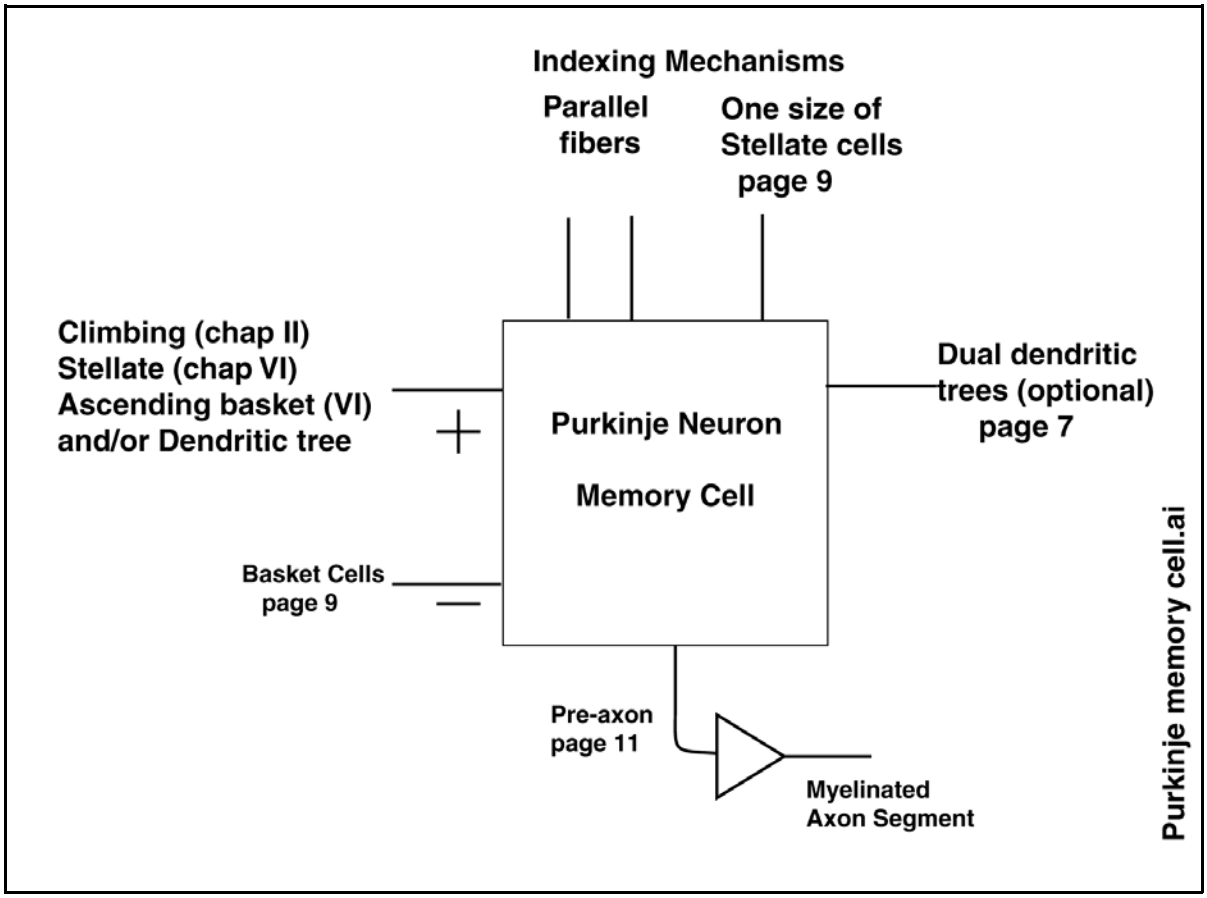


**Figure 17.6.1-9** A preliminary Purkinje memory cell EXPAND. Various names have been given to the signal paths supporting the memory cell as indicated at upper left. Page numbers refer to Eccles et al., 1967. See text and **Section 17.7.6**.

Like at the upper left, the definition of the neuron at upper right is not consistent in the literature. Some authors describe the neuron as a stellate cell while other authors describe the neuron as a basket cell. Still others describe basket cells as a particular size stellate cell.

In an alternate representation that is shown in the next figure, the assumption is made that the parts of the dendritic tree closest to the somaare, and the soma itself is, myelinated. If true, it is likely that the junction between the unmyelinated and myelinated portions of the dendritic tree is formed by a Node of Ranvier acting as a stage 3A pulse encoder. This area is worthy of further study to confirm whether action potentials are generated prior to the soma of the Purkinje cell. A similar situation is known to occur in the dendrites of neurons within the cochlear complex of the hearing modality (**Section xxx** of **PBH**). **Figure 17.6.1-10** shows a schematic of the major features of a potential Purkinje cell and its interfaces. This figure is expanded over that in **Section 10.2.5** to allow further detailing of the role of the adjacent neural circuits associated with the climbing, mossy and parallel fibers. These include the granule, basket, Golgi neurons. [xxx can show with or without electrical paths ] This figure does not show the axon extending from the lower pole of the neuron before becoming myelinated as reported above by Eccles et al. in 1967. It does show the Activa within the Purkinje neuron supporting multiple emitters, associated with multiple potential dendritic trees supporting the neuron as suggested by figures 10 and 40 of Palay & Chan-Palay. Whether the individual dendritic trees incorporate a stage 3A analog to pulse encoder as shown with a question mark, based on the suggestion of xxx that the primary dendritic segments become myelinated along with at least parts of the soma remains open to discussion.

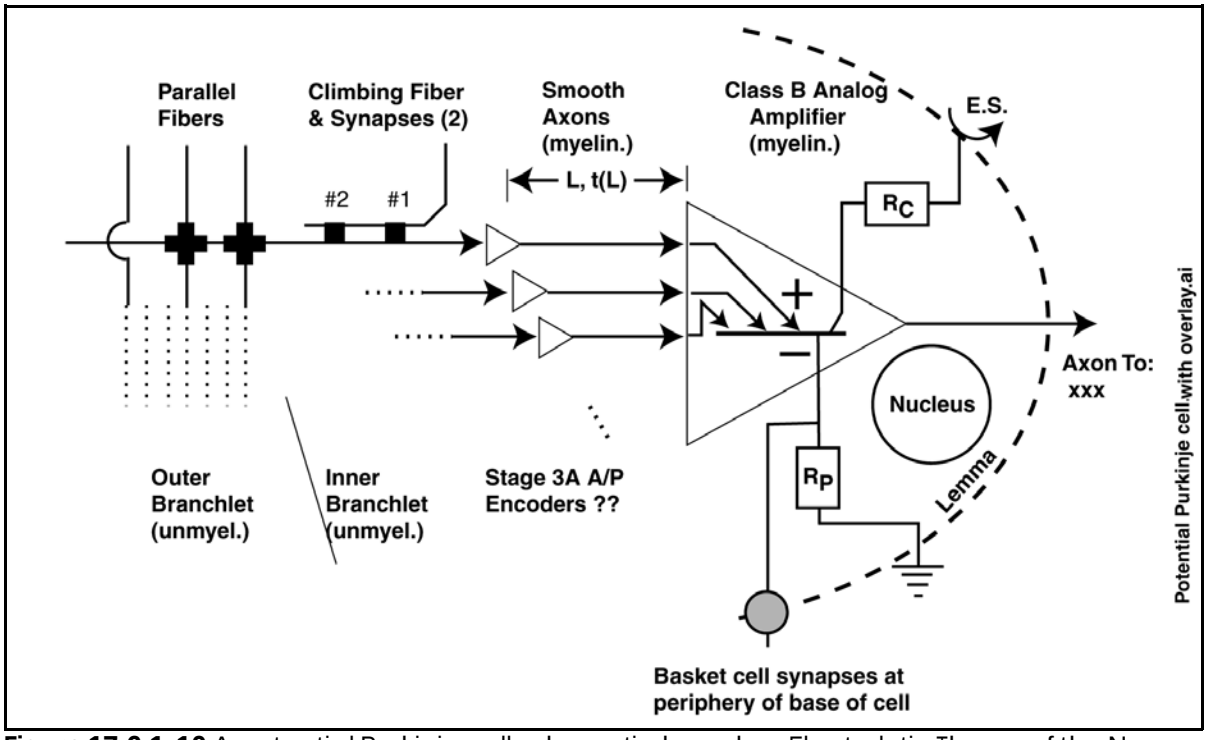


**Figure 17.6.1-10** A potential Purkinje cell schematic based on Electrolytic Theory of the Neuron ADD. All of the horizontal lines and features in this figure, except for the climbing fiber, are elements of a single Purkinje cell of the cerebellum. The cruciform connections shown may include active circuits associated with the parallel fibers, similar to a Node of Ranvier, as well as a synapse. The Activa within the Purkinje neuron is shown with multiple emitters, a common feature of man made semiconductor devices. See text.

This expansion

1, incorporates the parallel bar switching (**Section 10.2.5.4.4**) concept adopted to the neural environment,
2. recognizes that the indices represented by each parallel fiber can synapse with many individual dendritic branchlets of many Purkinje dendritic branches
3. recognizes that each of multiple dendritic branchlet can synapse with one or more of the parallel fibers of the parallel fibers penetrating the overall dendritic fan of one Purkinje cell,
4. recognizes the thin myelination of the stem portion of the dendritic tree associated with one Purkinje cell and the cell itself.
5. considers the possibility that the smooth portion of the "dendritic stem" might be a thinly myelinated axon following a stage 3A encoder within what appears at first glance to be a conventional dendritic tree.
6. asserts that all of the stage 3a analog to pulse encoders create positive going pulse trains that are applied to the non-inverting inputs of the class B (linear) amplifier of the Purkinje cell.
7. recognizes that the amplitude and timing of the inputs from the stage 3A encoders may be staggered and the output of the class B amplifier may exhibit a variable amplitude summation of overlapping pulses.
8. may include multiple synapses between each climbing fiber and a single inner branchlet of the dendritic tree, where the distance of each synapse from the stage 3A encoder associated with that branchlet may introduce a significant time delay.
9. recognizes that the total number of parallel fiber indices penetrating the dendritic fan of a single Purkinje cell may be in the range of 200,000 to 300,000.
10. may include one or more parallel fibers acting as indices and synapsing (shown by the cruciforms) with a given outer branchlet of a given dendritic branch.
11. accepts estimates by other investigators that as many as 50 parallel fibers may form cruciform connections with a single purkinje cell dendritic fan.
12. accepts the potential for axons from various other cell types (basket, stellate, etc.)to synapse with the

inverting input terminal of the Purkinje cell as either axonal-basilar dendritic (actually poditic) or axonal-somatic synapses.

[xxx expand list to include electrolytic parameters ]

- - - -

Palay & Chan-Palay (page 25) have noted the *absence* of a morphologically defined hillock in the vicinity of the emergent axon in the Purkinje cell. It may be necessary to explore the internal lemma of the Purkinje cell to locate a potential Activa, probably operating in the analog domain. The lemma is so thin, this may be a laborious search. On page 49, they provide a detailed structure of the initial axon segment that is compatible with the above figure. **Figure 17.6.1-11** shows multiple tubular channels within the soma of the Purkinje neuron, based on the electron microscopy of the investigators, extending to the root of the initial axon segment where they each synapses with that segment. This configuration suggests a multiple input structure for the Activa located at this location within the Purkinje neuron. This multiple emitter structure is incorporated into the previous figure based on this representation. This modified Activa structure is located at the location expected for a hillock but the volume of the Purkinje neuron may prevent its morphological identification.

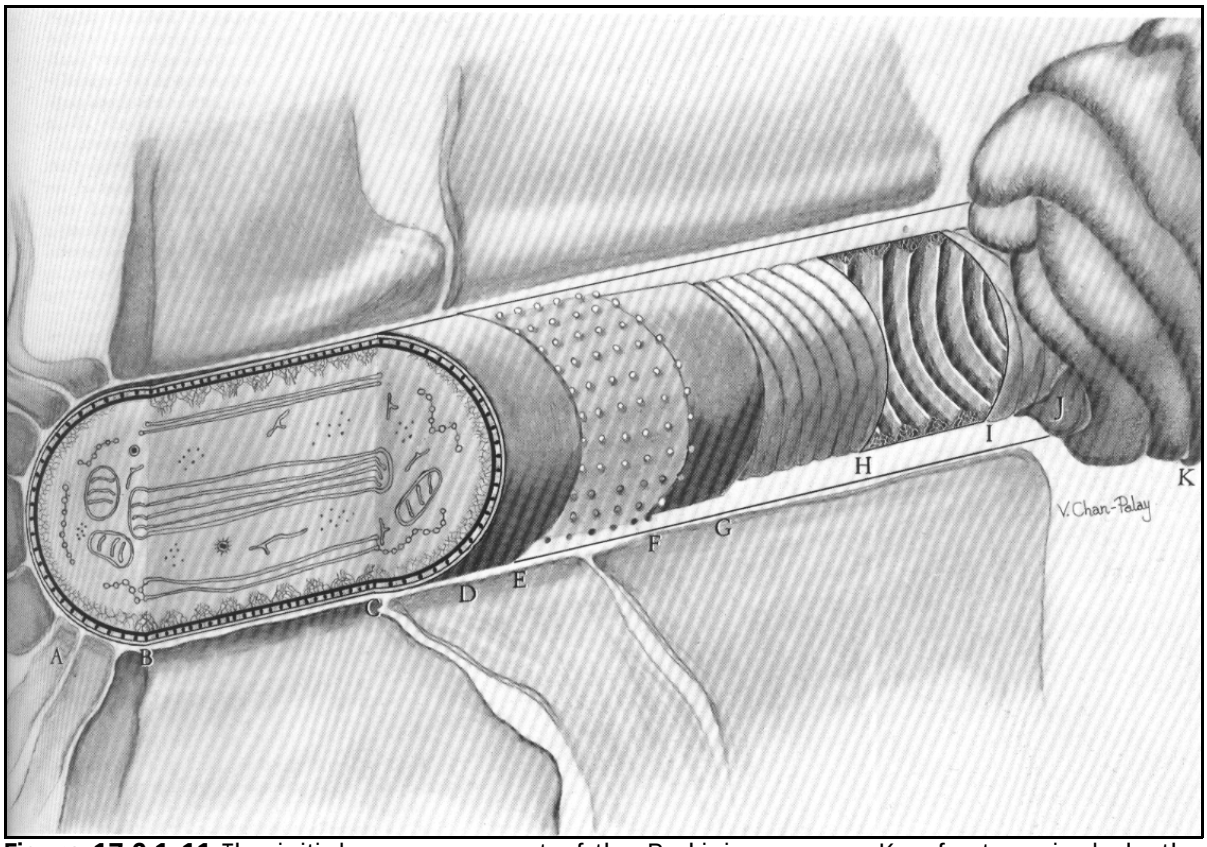


**Figure 17.6.1-11** The initial axon segment of the Purkinje neuron. Key features include the multiple independent connexions between apparently independent dendritic inputs on the left, A, and the launch mechanism (F–H), the electro-mechanical structure on the interior of the axon segment supporting the conversion of the signal to the propagation mode prior to the start of the matching section of the myelin sheath, K. See text for additional labels and discussion. From Palay & Chan-Palay, 1974

The complete caption of figure 40 of Palay & Chan-Palay is,

> "The tripartite undercoat of initial segments in Purkinje cell axons. This initial segment begins on the left where it is seen cut first in cross section (*A–B*), then in longitudinal section (B–C), and then again in cross section (*C–D*). Here the characteristic features of the tripartite undercoat, are diagrammed in cross section and longitudinal section. Beginning with the plasmalemma (*D–E*), each lamina is peeled off to reveal the next one lying beneath it, thus exposing the three components of the undercoat (*F–H*). For purposes of clarity, the drawing was not made to scale."

(H–I) of the figure suggest a launcher similar to that frequently found in electro-magnetic waveguides and antennas. The rings would be spaced at one wavelength, or one-half of a wavelength, intervals to the expected wavelength of the signal propagated over the myelinated portion of the axon segment. This launcher structure may be identified in Palay & Chan-Palay for the first time. Their representation will be incorporated into Chapter 9 of this work. The structure illustrated can be compared to that of a conventional axon segment shown in Figure 14.5.3-3 in **"Processes in Biological Vision," PBV** or Section 7.4.4 in "**Processes in Biological Hearing**," **PBH**.

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## 17.6.2 Diagrams related to the Limbic System EMPTY

Most of the figures in the academic literature relating to the Limbic System originated as pedagogical tools. **Figure 17.6.2-1** is one of these; it is used here for orientation purposes. For purposes of this work, the Limbic System stands alone and is not part of the cerebral cortex. It receives signals from many regions of both the cerebral cortex and the diencephalon, signals to the amygdala frequently associated with the Alarm Mode of the sensory modalities. It is believed that the hippocampus is the entry to the engines of long-term memory and it may be the location of short-term (working) memory. The engines of long-term memory are primarily housed in the cerebellum.

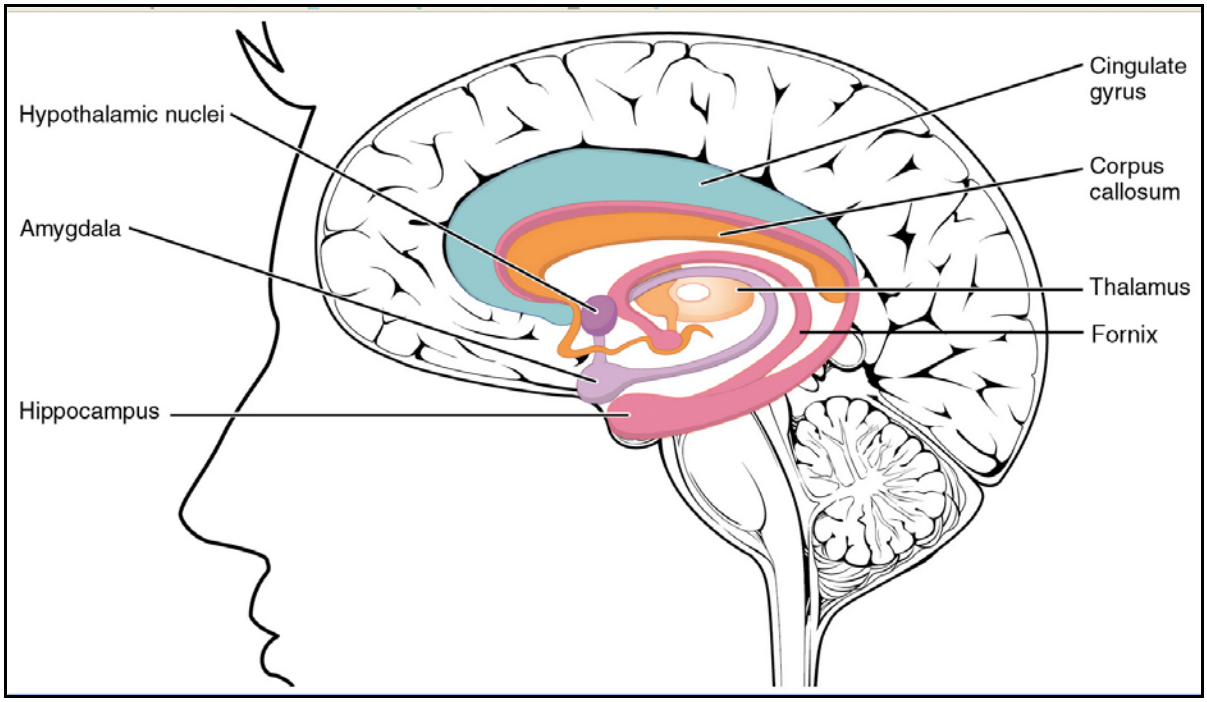


**Figure 17.6.2-1** The Limbic System for orientation . It is an entity located between the cerebral cortex and the diencephalon of the brainstem. The diencephalon is dominated by the thalamus but also includes the basal ganglia. The inner loop leaving the hippocampus is labeled the fornix.

### 17.6.2.3 Circuit level diagrams related to the Limbic System

There are a variety of circuit diagrams related to the cerebellum in the literature and on the internet. They are generally inconsistent, avoid describing the source and target of the signals passing through these circuits. do no show the character and polarity of intermediate signals, and are invariably based on the chemical theory of the neuron[84,85]. They do not demonstrate how memories are acquired, maintained or updated within the cerebellum.

[xxx [provide a better circuit diagram

## 17.6.3 Clues to memory level neural circuits

A review of the above **Section 17.5** and **Section 2.7.7** has surfaced a variety of circuit features that may help define the mechanisms providing the creation, storage, recall and update of memory. The reports of mossy fiber sprouting in relation to epilepsy (**Section 2.7.7.2.3**) may be particularly relevant.

The spacing of the Purkinje cells, the parallel fibers described and the potential equal spacing of the distance between the synapse of the parallel fibers and the Purkinje cells in **Section 2.7.7** suggest a synchronization function. This type of synchronization function is commonly required in any word serial/bit parallel encoding system prior to signal projection, whether by conduction or by propagation.

By employing several parallel fibers connecting multiple Purkinje cells as shown in [Figure 2.7.7-3, Multiple different operating states could be established before generating a word serial/bit parallel signal. This arrangement could allow a given group of Purkinje cells to create, store, recall and update multiple memory elements within one set of neurons.

If the parallel fibers do constitute an element in a synchronization mechanism, there is no requirement that nearby Purkinje cells fire simultaneously. Their generation of a pulse could be staggered in time, as long as the firing times were repeatable. The variation in timing could be compensated for as it is in Meyer's loops of the visual modality (Section xxx). Alternately, the variation in pulse timing among a group of Purkinje cells could constitute an element in a calculation employing computational anatomy.

The circuits surrounding the Purkinje cells in the cerebellum found in the literature, although not creditable at the detailed level, [xxx see Wisconsin_circuit diagram_cerebellum.wpg and compare it to the more explicit diagram of the Neurotransporter Group ] do suggest a feedback situation between the Purkinje cell and a Golgi cell or a basket cell. If confirmed in the near future, these circuit arrangements could constitute a "latching circuit" that could constitute a memory bit. Such arrangements are common in the electrical engineering domain.

### 17.6.3.1 The Inferior Olive as the Executive of the Cerebellum- Walberg 1956

Walberg, working primarily with cats, performed extensive histology on the inferior olive[86]. The information content of this paper is exceedingly dense. However, Walberg was not able to subdivide many of the tracts he identified in terms of the fascicules contained therein. This was a particular problem with regard to the "thalmo-olivary tract."

> Walberg noted, "As concerns descending fibers to the inferior olive from the thalamic nuclei and the basal ganglia, many conflicting views have been set forth, The concept of the "thalamo-olivary tract, ' is quite old and controversial. "the results of later investigations tend to support the assumption that thalamo-olivary fibers do not exist." Yet he used this designation throughout his paper.

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[84][xxx ]

[85][xxx ]

[86]Walberg, F. (1956) Descending Connections to the Inferior Olive *J Comp Neurol* vol 104(1), pp 77-173

The analysis below is limited primarily to pages 131 to165 of a 96 page paper. The inferior olive is a major component of the Interposed Neurons found within the white space of the cerebellum. Walberg's investigations on cats were necessarily focused on the skeleto-muscular elements of the neural system. He was not in a position, in his time, to differentiate the direction of travel of the signals definitively over most of the fascicules he identified. His indications of direction are primarily conceptual. Walberg did note, "The results of the present study make clear that the olive is organized in a more complex manner that has hitherto been realized." He then emphasized this fact by noting, "The structural and functional complexity of the inferior olive is certainly even greater than appears from the results of this study." In the context of this work, the inferior olive appears to play a role similar to that of the "control and switching" activities of the TRN in the broader context of the entire CNS. Three major functions of the inferior olive appear to involve,
1. the TRN requesting access to specific memories stored within the cerebellum,
2. the forwarding of such requested memories to the information extraction engines associated with the saliency map of stage 4,
3. the acceptance of instructions (in highly compact form) from stage 5A and 5B cognition engines and expanding those instructions into commands addressed to many neuro-muscular paths leading to many muscles operating in unison, frequently on a time staggered basis to achieve suitably smooth apparent motion of the limb, face or complete body.

**Figure 17.6.3-1** attempts to organize the detailed comments of Walberg into a schematic or block diagram combined with signal flow information. It will not address the apparent reflex activities associated with neural signals from the afferent side of the diagram (at lower left) and the efferent side (at lower right).

> Such reflex signals appear to be passed through the cerebellum in order to minimize delay times (latencies) associated with crucial defense mechanisms (and including those mechanisms that have been incorporated into various sports endeavors of humans.

Walberg's investigations did not involve the afferent sensory tracts nor the operations relating to the pre-frontal cortex initiating neural activity. These omissions leave the lower left and upper right portions of the figure to rely on earlier analyses within this work.

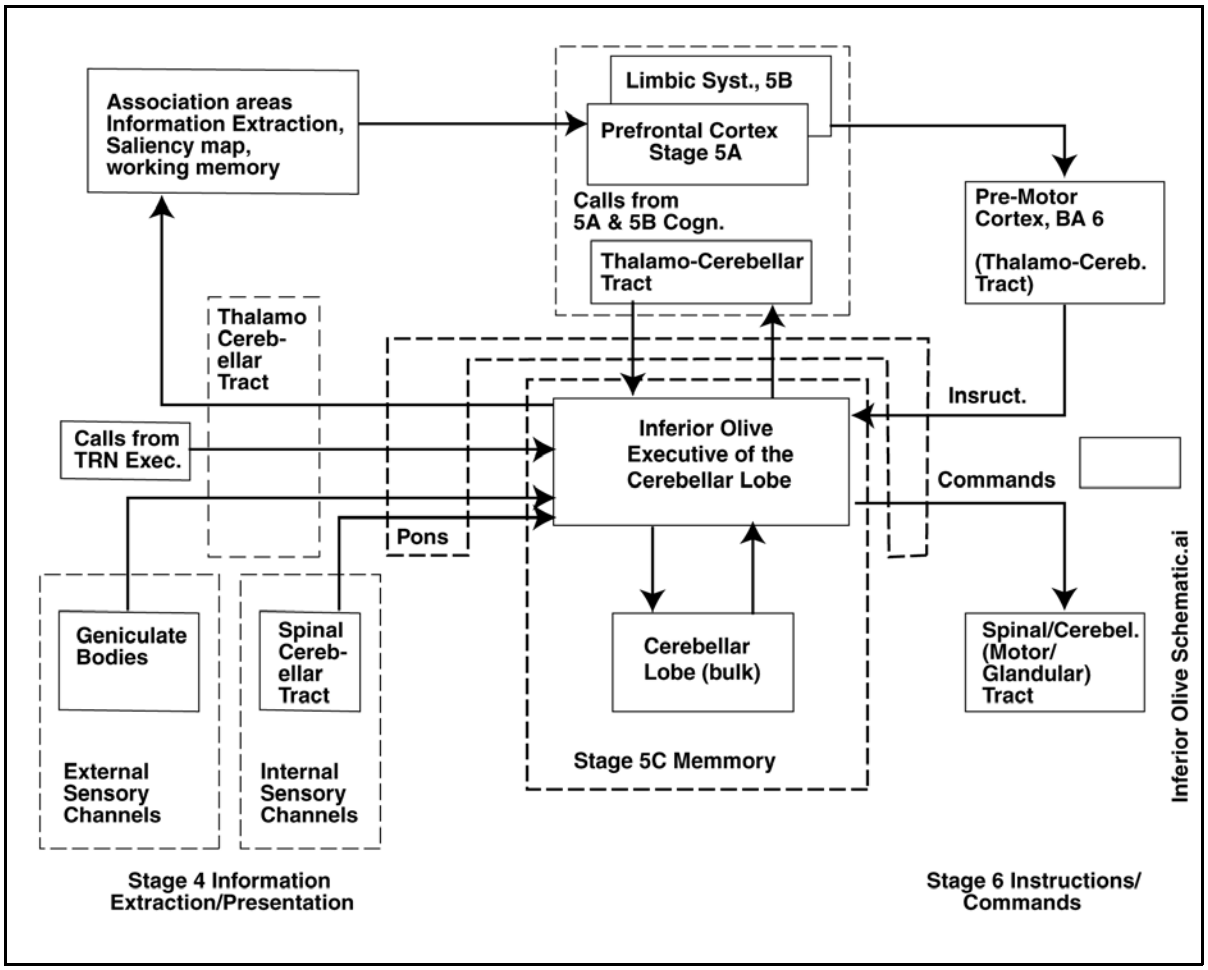


**Figure 17.6.3-1** Schematic of the Cerebellum & its interactions with other engines of the CNS. Walberg was unable to differentiate the fascicules within the thalmo-cerebellar tract adequately. The Pons is considered to be a "cable tray" to use the engineering term. It contains few if any signal processing neurons. This figure follows the figures of **Section 4.6.3** at the detail level. See text. Expanded from text of Walberg, 1956.

This diagram has expanded on Walberg's text to include the engines of stage 5 Cognition and the external sensory modalities within the context of Walberg's concept. It places the inferior olive in a central role with respect to the cerebellum similar to that of a portion of the TRN dedicated to the executive functions controlling the routing of neural signals within the cerebrum. It appears to control the routing of neural signals within the cerebellum and the engines/neural tracts he found to be closely associated with the cerebellum. In line with the aside above concerning the thalamo-cerebellar tract, the tract with that label on the left is shown dashed because of the multiple (and important) fascicules within that "tract."

The role of the pons as a mere cable tray providing a home for a great many soma of neurons but little or no signal processing between neural signals passing through is still a subject of discussion. It cannot be completely resolved based on a two-terminal theory of the neuron. Brodal reviewed his interpretation in 1954 (pages 121–140)[87].

[87]Brodal, A. (1954) Afferent Cerebellar Connections *In* Jansen, J. & Brodal, A. *eds.* Aspects of cerebellar anatomy. Forlag, Oslo: Johan Grundt Tanum, Chapter 11

The above paragraph leads to a proposal of how the higher level "control mechanisms" of the neural system operate. **Figure 17.6.3-2** illustrates a block diagram applicable to the expanded concept. The concept remains based on the framework of **Section 17.1.2**. The figure has explicitly subdivided stage 5 cognition into three major portions, stage 5A, logical, stage 5B emotional and stage 5C central memory storage.

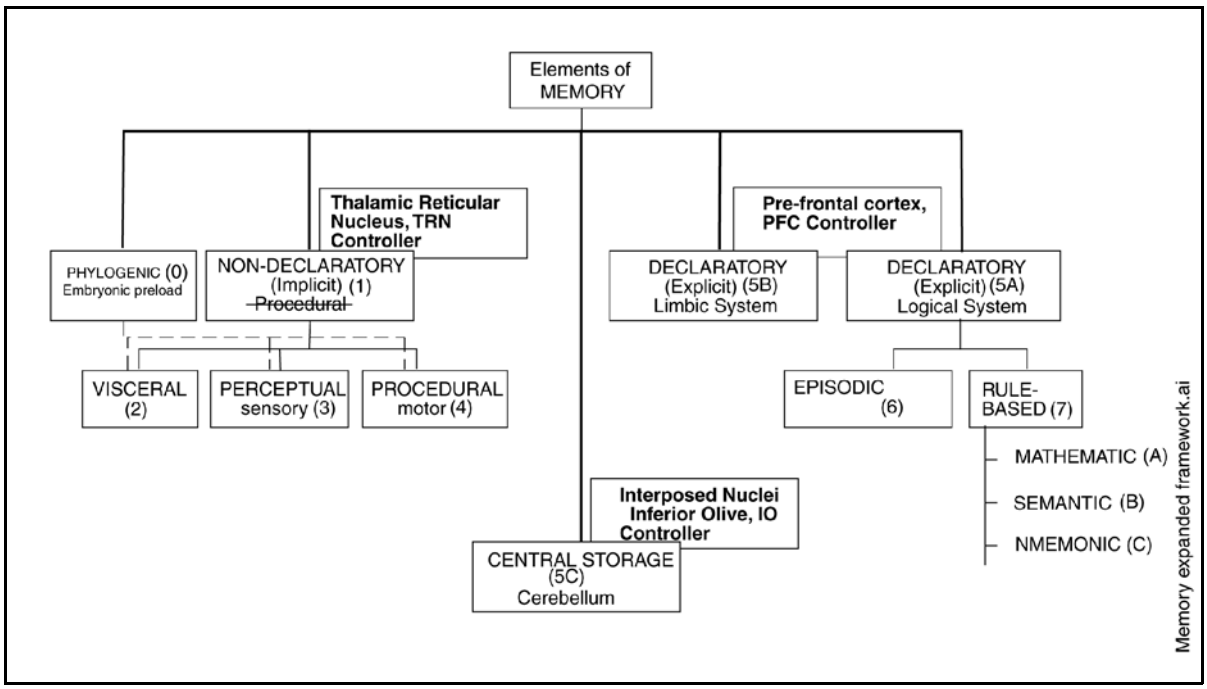


**Figure 17.6.3-2** Proposed (2018) high level control mechanisms of memory based on the distinction between declaratory and non-declaratory memory. The major controllers are shown offset and behind the major functional blocks. In many cases they would be shown in the direct path of signals they control. The PFC controller can request information from the internal executive, TRN, to retrieve configuration information that it can declare. See text and **Section 17.1.2**.

In a schematic or signal flow diagram of associated with the above block diagram, the controllers frequently appear in the direct path of signal flow while also carrying on switching and indexing functions (such as those associated with the parallel fibers of the Cerebellum). It may be appropriate, upon further analysis, to show one or more separate sub-controllers for the elements of the visceral system (particularly the cardiac and alimentary systems).

## 17.6.3.2 An atlas of the cerebellum in Talairach coordinates

**Section 10.2.3.3** describes the cerebellum from an historical perspective and then cites a recent atlas by Schmahmann et al. using "modern technology" to present the information in the coordinates of Talairach and Tournoux. Their MRI scanner was limited to a 1.5 T magnetic field. They noted, "This investigation was not specifically designed to study the detailed anatomy of the deep cerebellar nuclei (interposed nuclei). The outline of the nuclei characterized by the gray-white matter differentiation proved indistinct on these images.

Schmahmann et al. provided a Table 1 defining the major fissures of the Vermis Lobule and the Hemisphere Lobule. Their atlas also contained a cross-index (Table 2) to the terminology and nomenclature used by earlier morphology level investigators. It is reproduced here as **Figure 17.6.3-3** and in **Section 10.2.4.3**.

| Schmahmann et al. (1999) | Consensus | Dejerine (1901) | Bolk (1906) | Ingvar (1918, 1928) | Riley (1929) | Larsell (1936-1972) |
|---|---|---|---|---|---|---|
| **I,II** | lingula | lingula | 1 | lingula | lobulus I vermalis | I, II lingula |
| **III** | centralis | central | 2 | centralis | lobulus II vermalis | III centralis |
| **IV** | culmen [culmen of monticulus; culminis] | culmen | 3 | culmen | lobulus IV vermalis | IV culmen |
| **V** | | | 4 | | | V culmen |
| **VI** | declive [declive of monticulus; clivus monticuli; lobulus clivi] | déclive | lobulus simplex | simplex | lobulus C2 vermalis, pre-sulcal | VI declive |
| **VIIAf** | folium [folium of vermis; folium cacuminis] | bourgeon terminal | $C_2$ | lobulus medius | lobulus C2 vermalis, post-sulcal | VIIA folium/tuber |
| **VIIAt** | tuber [tuber of vermis; tuber valvulae] | tubercule valvulaire | | medianus | | |
| **VIIB** | caudal aspect of tuber valvulae | | | | | VIIB caudal aspect of tuber |
| **VIIIA** | pyramis | pyramide | $C_1$ | pyramis | lobulus C1 vermalis | VIIIA pyramis |
| **VIIIB** | | | | | | VIIIB pyramis |
| **IX** | uvula | luette | b | uvula | lobulus B vermalis | IX uvula |
| **X** | nodulus | nodule | a | nodulus | lobulus A vermalis | X nodulus |

**Figure 17.6.3-3** Cross-index of labels used to describe the cerebellum over time ADD. This is the first of two parts of the table. Also reproduced in its entirety in **Section 10.2.4.3**. From Schmahmann et al., 1999.

## 17.6.3.3 Further subdivision of the Inferior Olive

The text of Jansen& Brodal of 1954 is a very comprehensive summary of knowledge of cerebellar anatomy in 1954. While short in graphics, it is extensive in detailed discussions.

> On page 240, Jansen reviews the equivalence of terms between other mammals and man. "In all mammals with the exception of monotremes the cerebellar nuclei consist of a nucleus medialis, a nucleus interpositus and a nucleus lateralis. The nucleus medialis is presumably homologous with the nucleus fastigii, the nucleus interpositus with the globose and emboliform nuclei, and the nucleus lateralis with the nucleus dentatus in man."

On the same page, Jansen makes several other important summary remarks,

> All cortifugal fibers are formed by Purkinje cells. The short cortofugal fibers connect all parts of the

> cerebellar cortex with the cerebellar nuclei. The long cortifugal fibers, i.e. cortical fibers that pass beyond the cerebellar nuclei, are derived preponderantly and possibly exclusively from the cortex of the vermis and the flocculus. These fibers pass the cerebellar peduncle and terminate in the vestibular nuclei, . .."

The overall perception is that the cerebellum is quite directly connected to virtually all areas of the cerebrum and diencephalon in one way or another. A secondary perception is that there is a surprisingly tight linkage between the vestibular nuclei and the cerebellum. This may be in order to vary the stage 6 commands derived from the stage 5 instructions as the gravity vector changes relative to the animal. See specifically page 169.

Brodal & Jansen provided a finer study of the engines within the inferior olive and their connections highlighted in the above figure[88]. Xxx also have studied the interconnections of the inferior olive. **Figure 17.6.3-4** presents their primary graphic.

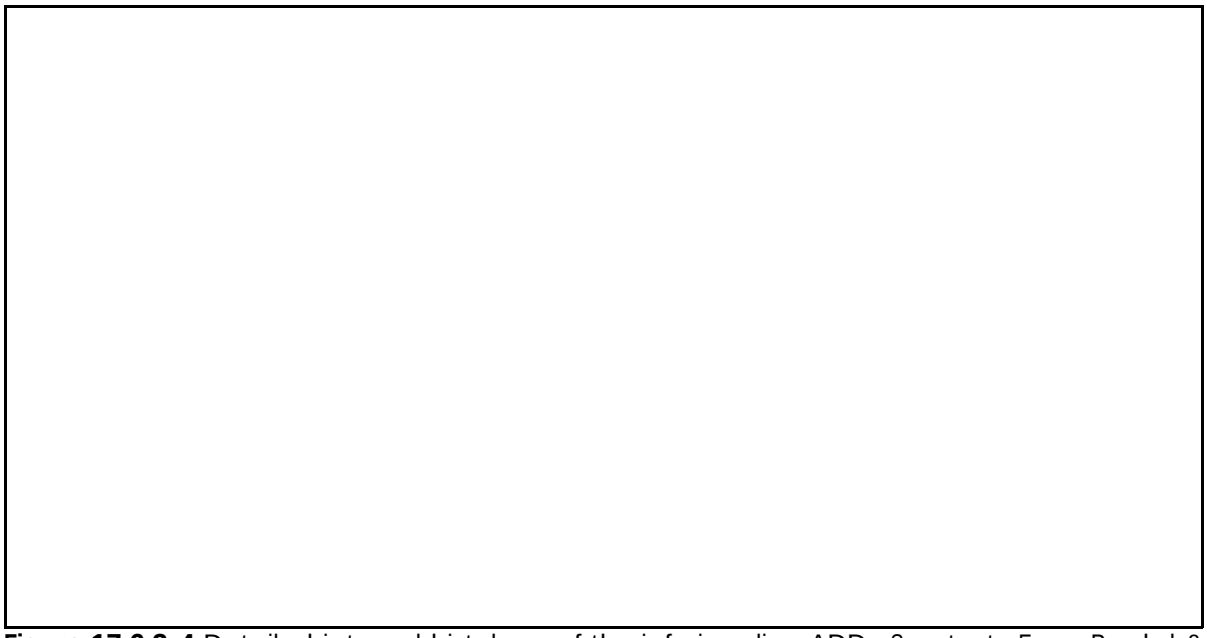

**Figure 17.6.3-4** Detailed internal histology of the inferior olive ADD. See text. From Brodal & Jansen, 1954.

Scheibel et al[89,90]. collected more data regarding signal flow in the interposed nuclei, and specifically the inferior olive in support of the 1956 Walberg paper. The 1955 paper provides information about the techniques they used and a variety of camera lucida images. They did not place these in an operational context. They did note, "The inferior olive has been found to contain two main types of cells differentiable primarily on the basis of their dendrite
arbor patterns. Those cells with straight comparatively unramified dendrite systems resembling reticular neurones have been found primarily in the caudal portions of the dorsal
and medial accessory olives whereas the more typical olivary neurones with highly ramified and spatially more limited dendrite arbors appear limited to the main olive nucleus and the rostral halves of the accessory nuclei."

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[88]Brodal, A. & Jansen, J. (1954) Structural organization of the cerebellum *In* Jansen, J. & Brodal, A. *eds.* Aspects of cerebellar anatomy. Forlag, Oslo: Johan Grundt Tanum, 423 p

[89]Scheibel, M. Scheibel, A. (1955) The inferior olive. A Golgi study *J Comp Neurol* vol 102(1), pp 77-131

[90]Scheibel, M. Scheibel, A. Walberg, F. & Brodal, A. (1956 ) Areal distribution of axonal and dendritic patterns in inferior olive J Comp Neurol vol 106(1), pp 21-49

The long unramified dendrites are frequently found in striated neural material where they are active in correlation processes. The bulk of the paper deals with strictly morphological information conceptualized from the samples of Golgi stained material.

The 1956 paper by Scheibel et al. expanded on the limited virtue of the Golgi Method of staining neural tissue. "Interpretation of data always depends in part upon possible sources of error inherent in the methods. The fortuitous nature of Golgi impregnations makes negative data of doubtful value. Structures can be identified and described with great precision when they appear in a preparation. However, the number of such structures visualized bears no necessary relation to the number actually present although trends may be established after examination of a sufficiently extensive body of material.

A second source of possible error rests in the fact that Golgi analyses are limited, at least in heavily myelinated areas such as the brain stem, to young animals between the first day and the second or third week of life.

In addition, we have observed that the rosettes themselves, like the mossy fiber terminals in the cerebellum, are seldom well developed in the first days of life. Therefore, identification may be difficult in the youngest preparations and indeed appreciable numbers of elements have had to be ignored or discarded because of such difficulties.

Mention is also made of difficulties inherent in identification of specific portions of the olivary complex as shown in lightly impregnated Golgi preparations (which are most favorable for identification of individual fibers) especially in horizontal and sagittal sections.

Because of the difficulties stated above, some olivary areas are excluded from full consideration. For this reason, the ventrolateral outgrowth will not be discussed at all in the text."

Clearly the two Scheibel papers should not be relied upon, except to corroborate other investigations. The Golgi Method should be considered archaic if not totally obsolete.

### 17.6.3.4 The Inferior Olive as the Executive of the Cerebellum- 1999

### 17.6.3.5 MRI experiments to find the location of memory storage

Initial PET and MRI experiments to determine the location of memory storage have been performed by Reinhold et al[91]. **Figure 17.6.3-5** shows an example of their early work. The obvious conclusion is that the cerebellum is involved in storing memories in their experiments. The other recorded locations may or may not be related to memory storage. They are more likely related to stage 4 information extraction related to the stimulus, and stage 5 prefrontal cortex activity related to what instruction the subject was given.

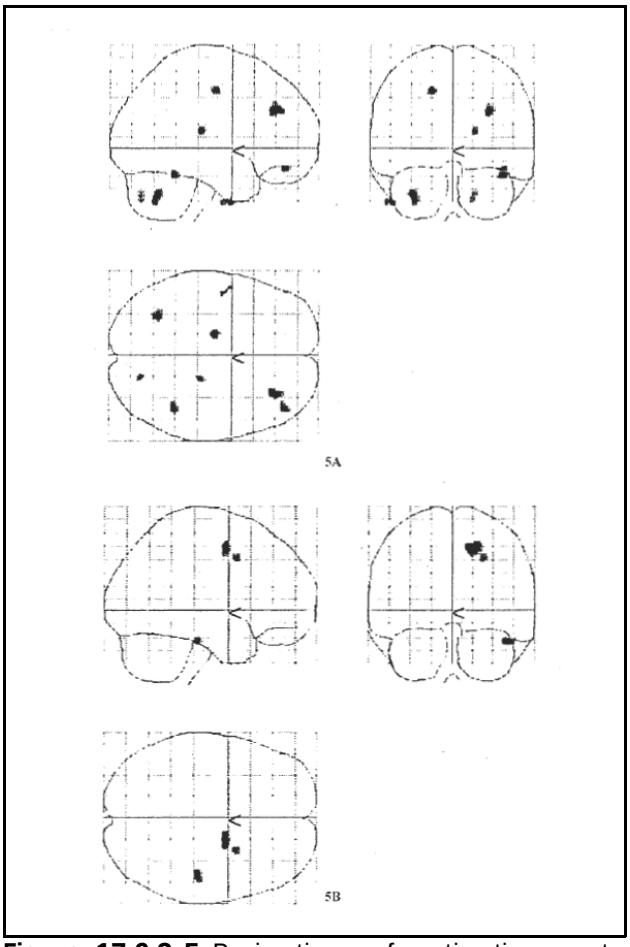


**Figure 17.6.3-5** Projections of activations onto representations of the standard stereotactic space (SPM99 glass brains). In (A), KL's activation pattern of retrieval of episodes from the amnesic time period relative to the non-amnesic time is presented showing activations (P ~ 0.001 uncorrected) in left cerebellum and right dorsolateral prefrontal cortex. In (B), the reverse contrast (episodes form the non-amnesic time) is shown, demonstrating activations in the right-sided medial frontal region and right cingulate gyrus. From Reinhold et al., 2006.

## 17.6.4 First documentation of the PNP Activa in a synapse

[xxx duplicate in section 10.2.4.xxx ]

As developed in **Section 10.2.4** and **Section 17.xxx**, Eccles et al. provided a significant and far

[91]Reinhold, N. Kuehnel, S. , M. & Markowitsch, H. (2006) Functional Neuroimaging in Memory and Memory Disturbances *Cur Med Imaging Rev* vol 2, pp 35-57

ranging text in 1967[92]. This text included a variety of electron micrographs based on the use of different "staining agents." They cited Herndon[93] of 1963. Figures 6 & 7 in that paper showing electron micrographs of axodendritic and axosomatic synapses on the surface of a Purkinje cell "after perfusion fixation with buffered osmium tetroxide" stain. This stain highlighted the line between the presynaptic and post synaptic surfaces of the synapses. It is proposed that the line constitutes the first documentation of the central or base region of a PNP Activa. ***This early documentation provides strong confirmation of the Electrolytic Theory of the Neuron as an electrolytic device, an active liquid crystalline semiconducting device.*** This documentation occurred within less than two decades of the discovery of the solid state semiconductor, the transistor, by man and not long after the introduction of the RCA EMU 3E electron microscope. It is not surprising the PNP Activa was not identified by that time.

**Figure 17.6.4-1** reproduces the original Herndon figures.

[92]Eccles, J. Ito, M. & Szentagothai, J. (1967) The Cerebellum as a Neuronal Machine. NY: Springer-Verlag *reprinted 2013*

[93]Herndon, R. (1963) The fine structure of the Purkinje cell *J Cell Biol* vol 18, pp 167-180

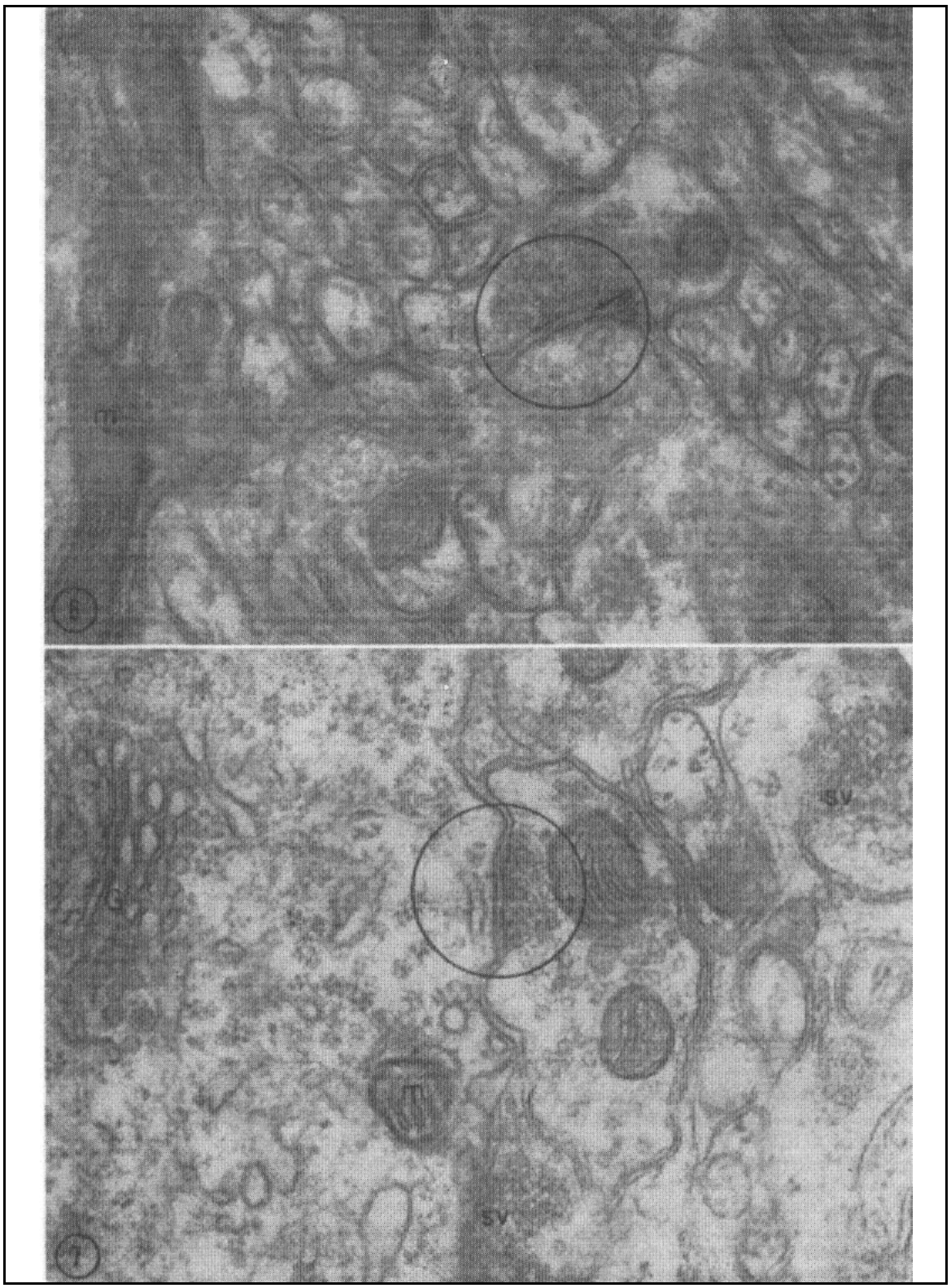


**Figure 17.6.4-1** Electron micrograph showing the base region of the PNP synapses of a Purkinje cell. See text for original captions and discussion. Copied from Internet Journal. See original publication for higher resolution imagery. From Herndon, 1963.

The original captions for the upper frame (Herndon fig 6) and the lower frame (Herndon fig 7) were as follows,

"Figure 6

Near the center of this micrograph is an axodendritic synapse (circled). The terminal axonal enlargement, which is above, contains numerous synaptic vesicles, and a mitochondrion is readily seen. Between the presynaptic and postsynaptic membranes, a thin dense line (arrow) can be seen. At the left is a secondary branch of a Purkinje cell dendrite which contains a mitochondrion at *m*. The origin of the dendritic spine making synaptic contact is out of the plane of section. X 42,000.

Figure 7

This micrograph shows an axosomatic synapse (circled). Near the center of the figure is the enlarged synaptic terminal (probably of a basket cell) containing two mitochondria and numerous synaptic vesicles clustered about the presynaptic membrane. To the left is the Purkinje cell cytoplasm. At the far left, elements of the Golgi apparatus (*G*) are seen. Mitochondrion, *m*; synaptic vesicles, *sv*. X 40,000."

> ***The chemical theory of the neuron has a difficult challenge explaining a substantial element between the pre and post synaptic membranes of a synapse.*** On the other hand, the Electrolytic Theory of the Neuron expects such an element to be in that location; it is expected to be a liquid crystalline form of water that forms an effective barrier against chemicals crossing the barrier while electronic charges move freely through it.

## 17.7 The Emerging Architecture of stages 4, 5 & 6 (After 2017)

With the growing understanding of how memories are stored, at both the circuit schematic level and the detailed storage circuit level, it is appropriate to recognize additional roles not incorporated in the architecture of **Section 4.6.3**. The expansion focuses on the subdivision of stage 5 cognition into stage 5A logical cognition, stage 5B emotional cognition, and 5C central memory in support of stages 5A & 5B. It also includes expanded understanding of the architecture of the Limbic System. The schematics in **Section 4.6.3** was originally developed based on the operations of what are defined here as logical cognition, as opposed to emotional cognition. When incorporating more elements of emotional cognition, it appears appropriate to introduce some alternate signaling paths. As the approach has evolved, it has called for the division of stage 5 cognition to be divided into three parts, stage 5A logical cognition, stage 5B emotional cognition and stage 5C memory devoted to memory engines supporting stages 5A & 5B. **Figure 17.7.1-1** is an expansion of those in **Section 4.6.3**. The proposal #5 and higher reflect the *long-sought* defining of the functional role of the basal ganglia within the neural system. The work of the Percheron and colleagues after the turn of the Century has resulted in the these changes (section 15.8.5 in "**Processes in Biological Vision**." [make hyperlink xxx ] Percheron defined a dual role for the striatum, he delineated by defining two distinct "territories" within the morphology of the striatum.

Here the first territory is labeled the "intellectual territory," and consists of the portion of the caudate nucleus and the putamen engines responsible for assembling the various association areas of the sensory modalities into a single composite saliency map. It appears the putamen, which is comparible in size with the pulvinar, is the principle memory engine associated with the saliency map and may qualify for the major source of "working memory" within the human neural system.

> The comparative positions of the saliency map supporting the path to the intellectual activity within stage 5 Cognition, and the direct path from the association areas to the limbic system maycontribute to explaining why the emotions of an individual occur largely independent of the intellectual state of the same individual. It may also help explain why the emotional state of the individual is not effectively stored in working memory, and is not transferred to long term memory.

The second, labeled the "sensory-motor territory" appears to perform a role similar to that of the cerebellum for the nonconscious executive described in **Section xxx**. The sensory-motor territory appears to provide a learning capability based on *intellectual activity* in contrast to the learning capability of the cerebellum that is focused on *non-intellectual activity*.

Although still tentative, it appears the putamen of the basal ganglia projects directly to the PFC with an entry point at the dorsolateral PFC, the dlPFC, designated by Brodmann Areas 9 and 46.

The complete development of these changes to the neural system schematic appears in section 15.8 in "**Processes in Biological Vision**." [make hyperlink xxx ]. See also **Section 4.6.4** in this work.

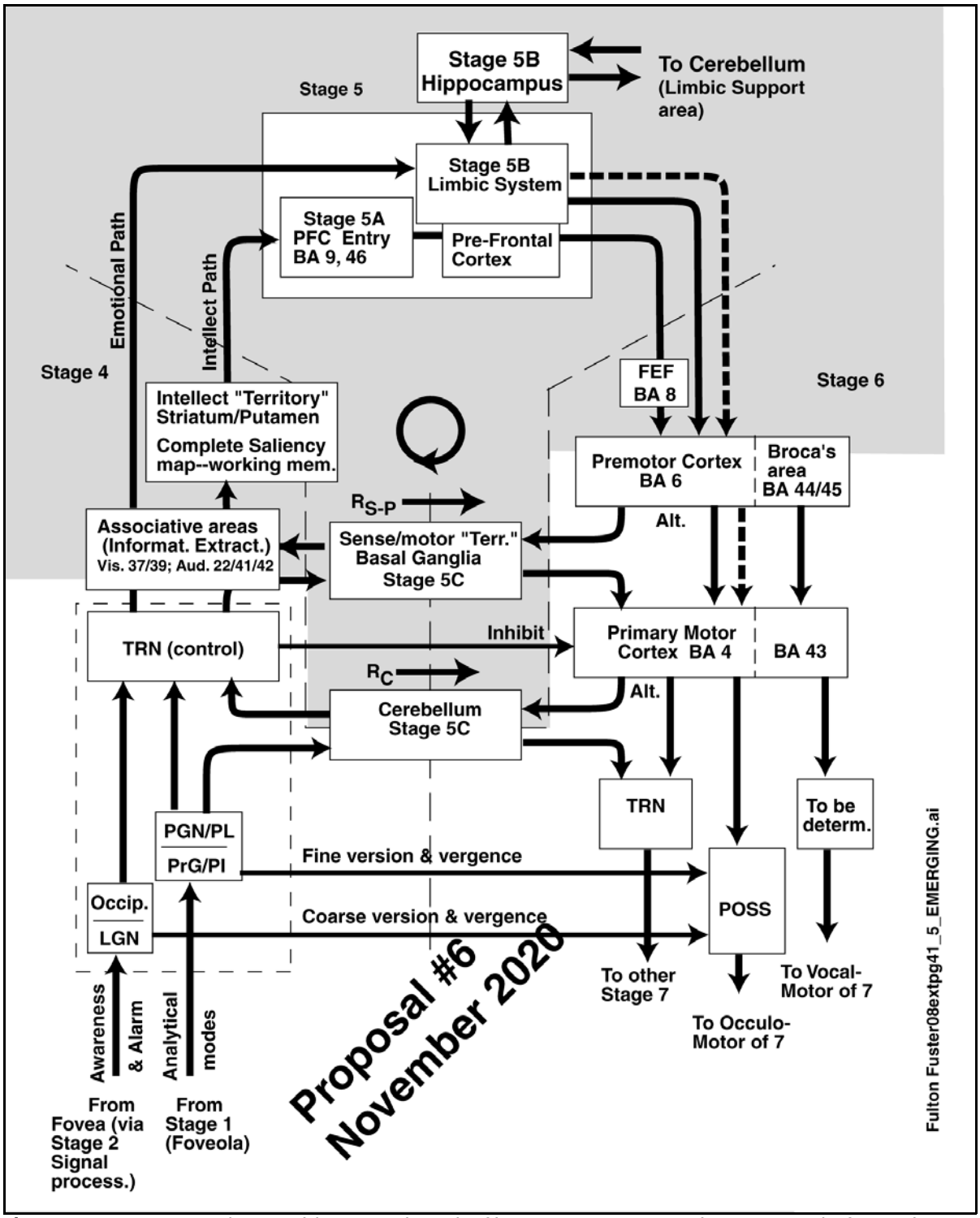


**Figure 17.7.1-1** Emerging Architecture (2017) of human CNS ADD. The proposal of March 2020 reflects the definition of two "Territories" of the basal ganglia as significant players in the neural system of humans. What does the dashed line at upper right signify? FEF, frontal eye field. See text.

There are indications, based on the cited papers and the discussions of this work, that Stage 5B may include an element within or similar to the expanded working memory, shown on the left in the above figure, dedicated to stage 5A.

Proposal #6 incorporates gathering knowledge of the role of the hippocampus in short-term memory supporting stage 5 operations and possibly the major conduit of memories to be stored and recalled from permanent memory within the cerebellum (**Section 17.2.2**).

The journal "Hippocampus" produced a special issue summarizing our knowledge of the Hippocampal formation as of 2000[94]. It is worthy of review and several of its articles will be cited below. However, much of this knowledge arises from more recent research into dementia among the elderly and Alzheimers Disease.

When this work begins to discuss the circuitry surrounding the Purkinje neuron in support of stage 5C memory operations (**Section 17.7.4** and **Section 17.7.5**), the paper of Szentagothai of (1965) is critically important. Except for his one major assumption based on the reigning chemical theory of the day that excitatory and inhibitory signaling were directly related to the axons of the presynaptic element, his results are nearly identical to those arrived at in this work (in much greater detail). The scope of his paper will be discussed in **Section 17.7.6.xxx**.

## 17.7.1 The expanded definition of a Memory Trace xxx

Section 17.2.2 discusses the concept of a memory trace that can be used to recall a given memory by Rudy and subsequently revised and expanded by others.
[xxx consider how to include metadata in this concept.

### 17.7.1.1 Background related to the search and the approach adopted here

Rudy describes the general case of memory traces developed by psychologists in an earlier era (page 131).

In 2018, a feature news article reviewed the failure to confirmed most conceptually based descriptions of "a memory trace" through 2018[95]. The problem is primarily with the concepts not being placed in a broad enough context. They resurrect the work of McConnell during the 1959 time period. McConnell did not seem to recognize that many lower forms of animals do not have a centralized nervous system. Thus, cutting off the head of a worm, with a very simple distributed nervous system has little effect on its life cycle (**Section 4.2.2**). It apparently has no effect on what little memory it had. Saunders then proceeds to review the concept of an "engram" as a physical memory trace but then notes, "But the nature of these stable, specific imprints is a mystery." This led her to interpret the work during the 1980's related to the sea slug, Aplysia, and based on the chemical theory of the neuron. She quoted one of the primary researchers of that concept in 2018, "Until a few years ago, I implicitly accepted this model for memory, I don't anymore." Their concept was based on the concept of synapses being formed by the expansion of spines resulting in the formation of new synapses in some form of logical manner. "then the new contact points that appear when a memory is formed should be the same ones that vanish when the memory is subsequently lost. That is not what happened, —not even close. We found that it was totally random. Completely random." She went on to describe several more concepts, some introducing the ubiquitous in the biological sciences, based on the chemistry based neuron, the euphemistic "silent mechanism" and "occult memories," even introducing "muscular tissue" into a synapse. One of the researchers exploring the physical strength of synapses then noted, "That approach has produced about 12,000 or so papers in the topic, but it hasn't been very successful in explaining how memory works." The article closes with, "And still more engram ideas abound. Some results suggest that a protein called PKM-zeta, which helps keep synapses strong, preserves memories."

A new concept has recently arisen in the field of neurobiology as defined by Rudy in 2008 (**Section 17.1.1**). It has begun the process of attempting to define the character and extent of a memory trace with particular focus on declaratory memory **Section 17.2.5**).

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[94]Special Edition (2000) The Nature of Hippcampal-Cortical Interaction: Theoretical and Experimental Perspectives *Hippocampus* vol 10(4), pp 351-499

[95]Sanders, L. (2018) Traces of Memory. *Science News* 3 February, pp 22-26

This work has taken a different direction than Rudy. It has begun the process of identifying multiple "traces," at the schematic level, associated with the more complex mechanisms associated with both learning, memory and smooth physical and hormonal actions based on the Electrolytic Theory of the neuron (**Section 17.2.5.1**)as well as the emerging knowledge regarding the memory circuits potentially employed in the cerebellum (**Section 2.7.7**, **Section 4.3.6** and **Section 17.2.8**). This approach relates memory traces to the multiple steps within stages 4, 5 & 6 and involving object recognition, memory storage, memory recall, memory and updating. This approach supports both declaratory and non-declaratory memory.

A more focused **Figure 17.7.1-2** is provided to clarify the following memory traces.

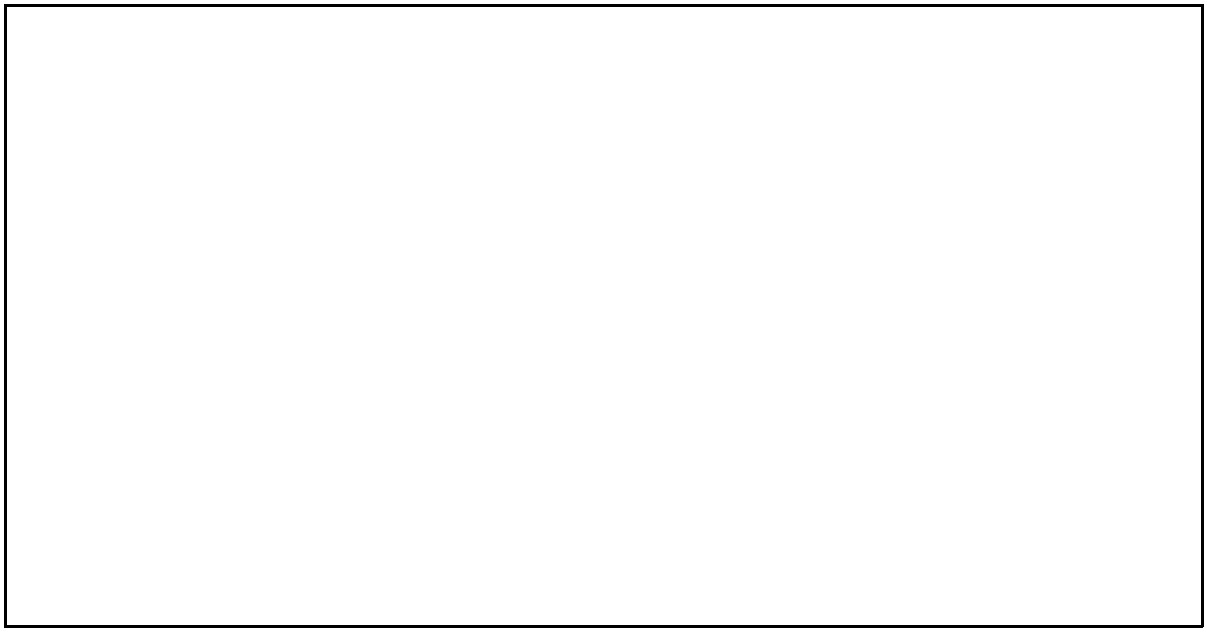

**Figure 17.7.1-2** Emerging Schematic focused on the memory traces involved in afferent learning & efferent actions EMPTY.

The definition of a memory trace can now be expanded. Following the architecture outlined in **Section 4.6.3**, and expanded in **Section 17.2.8**,

**Memory trace–** Any neural circuit path; 1) beginning with a stage 1 sensory receptor, passing through a memory storage path of stage 5C, and ending at one or more stage 6 neuroaffectors (thereby stimulating a muscular–skeletal response observable by the investigator **OR** 2) any neural circuit path beginning in stage 5A or 5B *de novo*, passing through a memory storage path of stage 5C, and ending at one or more stage 6 neuroaffectors (thereby stimulating a muscular–skeletal response observable by the investigator .

The above definition can be narrowed to include only the memory trace within the individual memory storage circuit. In that case, a state diagram may be useful to describe the operation of the circuit at different times during its operating cycle. The result may highlight multiple sequential memory trace paths through the memory storage circuit over a time interval to be determined.

As noted in **Section 17.1.4.4**, the anatomy and histology of the cerebellum has begun to take on the characteristics of a "cross-bar switch" developed in the 1940's for telephone circuit switching. Such switches have evolved from the original mechanical version to the recent all–electronic versions that exhibit a topology similar to that of the cerebellum.

If the assertion by Rudy (2008, page 257) is correct, that "the hippocampus does not actually store memories,"

its role and that of the amygdala relative to memory traces may be similar to that of the striadum and pallidum. This role would be conditioning information prior to its storage within the cerebellum or its extraction for comparison with current information concerning the environment [xxx Thus, the labels striatum and pallidum may be combined with xxx and xxx via the slash mark as shown in the above figure.]

### 17.7.1.1.1 The analogy between the cerebellum & man-made circuits

The next paragraph and figure also appear in **Section 10.2.4.4.3**.

The new approach also treats the cerebellum as similar to a large scale man-made field-programmable gate arrays (FPGAs) and application-specific integrated circuits (ASICs) that have evolved from programmable read-write memory. In general terms, FPGAs are programmable silicon chips with a collection of programmable logic blocks surrounded by Input/Output blocks that are put together through programmable interconnect resources to become any kind of digital circuit or system. FPGAs developed from programmable read-only memory (PROM) and programmable logic devices (PLDs)[96]. Quoting Bursky, "Each independent processing task is assigned to a dedicated section of the chip. Therefore, the performance of one part of the application is not affected when more processing tasks are added. ASICs[97] are similar to FPGAs but an earlier technology. Both of these devices exceed 10 million gates per chip in current production. The resulting memory cell density would be similar to, or smaller than, the size of a Purkinje neuron (25 microns diameter). Bursky has provided two architectures for the FPGAs. **Figure 17.7.1-3** shows his row-based architecture. The I/O blocks at top and bottom are very similar to a parallel bar switch (the parallel fiber network). The I/O blocks at left and right can be considered analogs of the descending fibers of the basket cells.

[96]Bursky, D (2016) The Principles of FPGAs. *Electronic Design* May 26th http://www.electronicdesign.com/fpgas/principles-fpgas

[97]Bursky, D (2002) Digital ICs: ASICs. *Electronic Design* January 6th http://www.electronicdesign.com/boards/digital-ics-asics

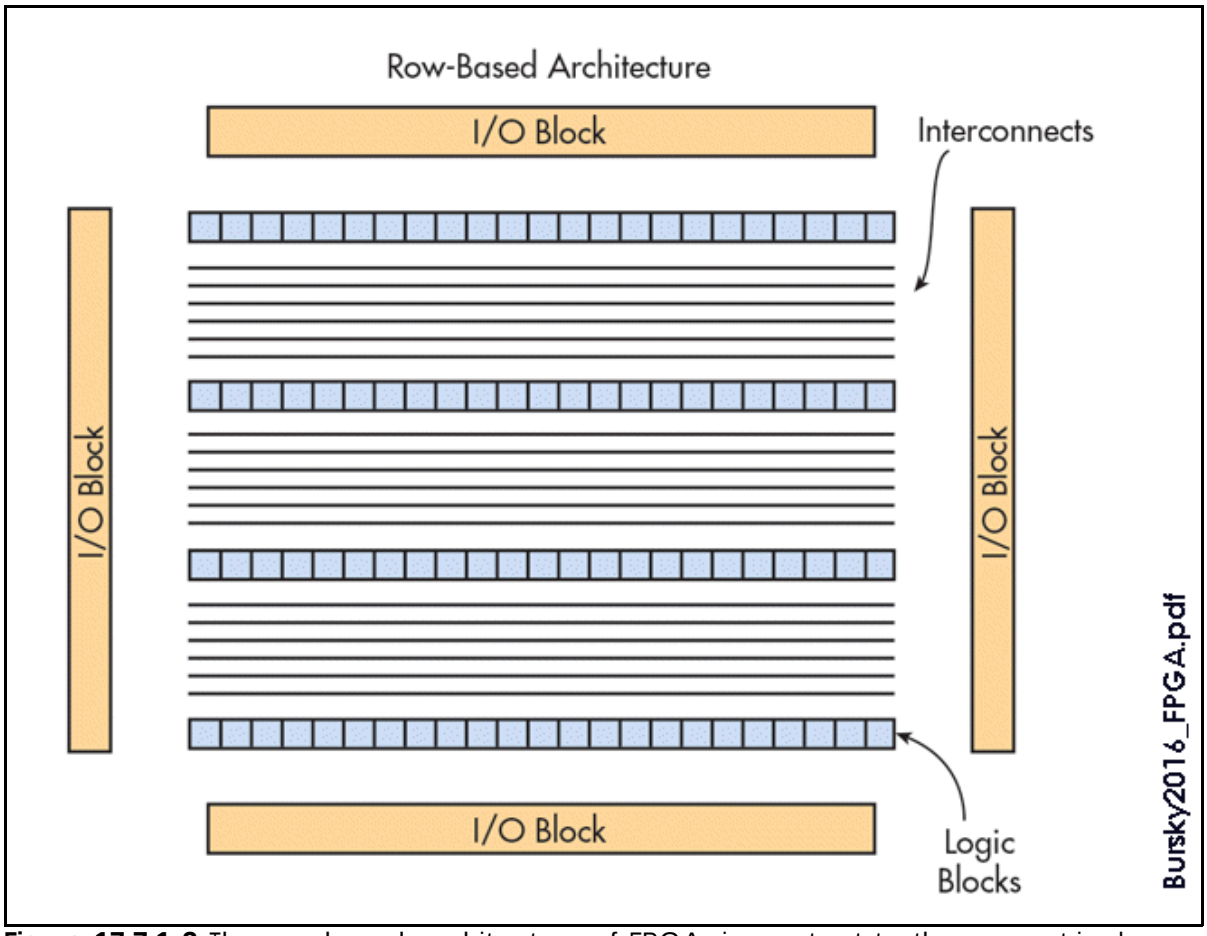


**Figure 17.7.1-3** The row-based architecture of FPGAs in contrast to the symmetrical array architecture. Either architecture is a candidate for the memory circuits of the cerebellum. Similar architectures are available in ASICs. The row-based architecture seems closest to the architecture surrounding Purkinje neurons acting as logic blocks. See text. From Bursky, 2016.

Unlike some man-made processors, FPGAs are truly parallel in nature. Each independent processing task is assigned to a dedicated section of the chip. Therefore, the performance of one part of the application is not affected when more processing tasks are added.

Bursky closes his 2002 paper by noting, “As the number of gates on a chip increases, so does power consumption. Lowering today's 2.5-V operating voltage to 1.5 V and even lower will grant designers significant reductions in power consumption.” When they can operate at 150 mV, they will be in competitive range with the memory devices of the animal brain. He also noted, “Still higher speeds are ahead, with clock rates beating 1 GHz and high-speed serial interfaces hitting the 5-GHz mark as on-chip gate dimensions drop below 0.10 μm” These speeds are far higher than ever required in biological circuitry. The gate dimension of 0.10 microns is compatible with the synapses diameter of biological devices.

### 17.7.1.2 A multiplicity of memory traces associated with learning

Generally, the encounter with any perception of the external environment can create a number of memory traces. These may involve multiple modalities and a variety of paths through the neural system depending on the experience of the subject. [xxx ADD ]

### 17.7.1.2.1 Afferent memory traces associated with matching existing memories

1. Beginning with the initial stimulation of any of the sensory modalities, an initial memory block is created that describes the perception of any object in the field brought to the subjects attention.

2. The TRN performs an initial review of that memory block. It then queries the combined long and short term memory in order to gain access to a variety of potential matches.

3. The TRN, or an engine associated with the saliency map or parietal lobe, attempts to match the perceived memory block and the stored memories.

4. If a match is obtained, possibly based on employing fuzzy logic, the engine responsible for the matching passes that meta data to the saliency map or on to the stage 5 cognition engines.

[xxx salvage ideas from the following trace is created representing the data from the sensory receptors of that modality and the TRN, which causes a search of stage 5C memory for a similar signal or pattern of signals. These patterns are compared in the initial associative areas of that modality. Different memory traces may result from this process. ]

### 17.7.1.2.2 Afferent memory traces associated with establishing new memories

5. If a match is not obtained, the raw perception is passed to the appropriate stage 5 cognition engines for additional information extraction.

6. Following information extraction from the unmatched perception, the stage 5 engine passes the new memory block via the stage 5 instruction path to the stage 5C circuits of the pallidum/hippocampal path to the cerebellum.

### 17.7.1.2.3 Memory traces associated with efferent signaling

When the stage 5 cognitive engines decide to instruct the body to take some action, it issues an instruction to the afferent engines, probably closely associated with the saliency map, to look up the necessary memory block(s) in order to convert the instruction to a broader group of commands that can be transimitted via the stage 6 neurons and implemented by the stage 7 muscular/hormonal elements.

1. If no satisfactory match of the representation of the current environment and the similar previously stored patterns, the current pattern is placed in the saliency map of stage 4, in a relatively raw form where it can be accessed by the stage 5 engines for more detailed information extraction. The result of that analysis is a more abstract representation that is then passed back to the stage 5C memory circuits for storage (and potential instructions to the stage 6 command engines).

### 17.7.1.2.4 Bypassing stages 5A & 5B when in familiar territory–practice

When a perceived representation is matched in the engines of stage 4, the metadata associated with this fact can be passed to stage 5 as noted above. However, there is another option if pre-approved by the cognitive engines of stage 5 is passed to the executive of the stage 4 TRN. The metadata can be transmitted to the stage 5C circuits of the cerebellum for immediate implementation by the muscular/hormonal engines of stage 7. This capability highlights the role of training, from the earliest age of the animal to the most skilled athletes of the species.

> Children of most species are endowed with a limited amount of programmed memory before birth. Thus learning, such as learning to hit a stationary ball on a stand leads to hitting a ball pitched to the

child. Later, his skill may improve to the professional level; this however, will require considerable and frequent practice to maintain the instruction to command conversion process optimized and the skeletal/muscular complex highly prepared to perform.

As a result of the above training, the transfer of meta data from afferent stage 4 to efferent stage 6 constitutes a ***reflex action at the highest level*** and explains why a professional athlete can make plays before his prefrontal cortex is even aware of the received perception and the physical response already taken.

## 17.7.2 The best current understanding of biological memory mechanisms

As is frequently found in the bioscience literature, the most recent papers on biological memory include many simple block diagrams. However, a majority of the connecting paths between engines or larger elements of the neural system are indicated by double arrow headed connections. This situation indicates the field is still in the exploratory research phase.

The first step in salvation from the double arrow situation can be found by reinterpreting al of the typical neurons, all but the stage 1 sensory neurons, as three-terminal devices. As such, they mimic the three terminal liquid crystalline semiconductor device inside of the neuron, the Activa. The Activa and the resultant neuron both exhibit a differential input structure. The apical neurite, the dendrite and its potential arborization provides a non-inverting signal input relative to the axonal output. The circumferential neurite, the podite and its potential arborization provides an inverting signal input relative to the axonal output. This reinterpretation intrinsically recognizes that the terms Glutoergic and GABAergic are obsolete and glutamate and GABA are actually involved in providing electrical power to the individual Activa in each neuron. The analog output of every axon is intrinsically bipolar. However, all stage 3 signal projection neurons are myelinated and produce positive going monopolar pulses.

A result of understanding the internal operation of the neuron, it becomes clear that there are no such synapses as dendro-dendro, dendro-soma or dendro-axon types. Neural signals are always orthodromic with two types of input ports and only one type of output port, although each type may be arborized to a considerable degree. All synapses, and Nodes of Ranvier, are intrinsically electrolytic devices built around an Activa with the same characteristics as the Activa within a three-terminal neuron. However, as in many man-made electronic circuits, they may be externally wired to operate as two terminal diodes.

Based on these baseline conditions, it is possible to determine the function and direction of most signal paths related to memory traces unambiguously.

Once the direction and character of a group of signal paths, and the nature of the circuitry of small groups of neurons within an engine devoted to the storage of individual memories, it becomes possible to explore possible memory storage circuit topologies. As of, 2017, ***this condition, based on the above reinterpretations, has not yet occurred.***

From the neurobioscience perspective, as opposed to the narrower and archaic neurobiology perspective (figure of **Section 17.1**), it then becomes possible to define the potential mechanisms of memory storage. Searching for this mechanism must avoid the Bayesian approach of limiting the available mechanisms to those familiar to a researcher trained in chemistry or biology. All possible approaches must be considered, even those that arise from the data reduction process that might appear as outliers to the investigator. Many of the most attractive approaches and mechanisms to be found in the realm of semiconductor based electronic devices.

In the case of information extraction and memory storage, the concepts of both fuzzy logic and truncated words/bytes must be considered viable until proven otherwise.

### 17.7.2.1 Potential electronic/electrolytic storage mechanisms EMPTY

[xxx consider delay lines, rotary disks, cross-wire and magnetic memories, and latches. ]
[xxx recognize the potential for mechanisms appropriate to groups of neurons with thousands of inputs to each neurite present. ]
[xxx consider multi-layer topologies becoming so common in multilayer circuit boards of even consumer destined electronics. ]
[xxx consider the temporal characteristics of each considered circuit. ]

## 17.7.2.2 Most likely storage mechanism configurations EMPTY

## 17.7.2.3 Potential organization of the memory database EMPTY

To appreciate the potential organization of memory, it is important to introduce the tools of library science into the neuroscience of the neural system (not the narrower neurobiology of the system, **Section 17.1**). Library science includes the study of potential labeling of data bytes, data bases, data reliability enhancement and data recall strategies.

In the library sciences, the term word is typically replaced by byte. The expression word serial/bit parallel becomes byte serial/bit parallel. The byte is frequently divided into segments, not unlike a chromosome, to serve different purposes. Associations between related bytes is frequently included within a segment of a byte. Estimates of the number of bits per byte could not be found in the literature. However, one potential number, 12-14 is described in **Section 17.7.5.1**.

Very few papers have appeared on the organization of the database(s) employed in the neural system. When addressed, the databases and word formats are usually only addressed at the conceptual level. The previous discussions of the Papez circuits and amygdaloid circuits are clearly at the conceptual level, as are other potential organizations of memory (**Section 17.2.2.1**).

Rudy has indirectly highlighted the fact that the organization and tools used to process different portions of neural memory (alternately distinctly different databases) may employ different tools displaying different time scales. Clearly many aspects of the database supporting the procedural portion of non-declaratory memory (**Section17.1.2**) must be recallable and compared with the current representation of the environment within small fractions of a second. Recall the baseball batter's requirement to evaluate the environment and cause the musculo-skeletal system to react in significantly less than one second.

Rudy has reviewed some of the potential theories of declaratory memory operation in his chapters 10 & 11. (**Section 17.2.5**). His Part 3, chapters 12 through 16, takes a broader view of the potential memory systems, mostly from a psychophysical perspective, as of 2008.

In his chapter 13, he has noted two alternatives in memory design and operation; "The Hierarchy and the Loop" on his page 255. The first accompanying figure has a conceptual input and no discernable output. The second figure exhibits no input or output elements.

> It is important to consider the definition of a loop very carefully. Ruby gives a brief definition of a loop on page 255 that suggest the information carried forward to the hippocampus is then passed back to the earlier engines of the hippocampal formation in the same form, thereby generating a loop with regard to information processing. However the information passed back may not be in the same form. It is necessary to develop a state diagram for the signals and information processed in order to understand the processes involved more clearly. The state diagram is particularly important in considering the learning process.

His text does define his interpretations of the processes involved in each type of operation within the hippocampal formation. On page 256, Rudy defines the elements of the hippocampal formation, sometimes referred to as the **medial temporal hippocampal (MTH) system**, as a hierarchal system serving the episodic portion of declaratory memory.

**Figure 17.7.2-1** expands block diagram of the hippocampal formation by putting it into context (his page 273 and beyond xxx). The original figure was based on Lavenex & Amaral[98], and Eichenbaum[99] in a special issue of "Hippocampus." This view is labeled the "Unitary view" as it combines the methodology associated with both episodic and semantic memory.

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[98]Lavenex, P., & Amaral, D. (2000). Hippocampal-neocortical interaction: A hierarchy of associativity. *Hippocampus* 10(4), 420-430. DOI: 10.1002/1098-1063(2000)10:4<420::AID-HIPO8>3.0.CO;2-5

[99]Eichenbaum, H. (2000) A Cortical–hippocampal System For Declarative Memory *Nature Rev: Neurosci* vol 1, pp 41-50

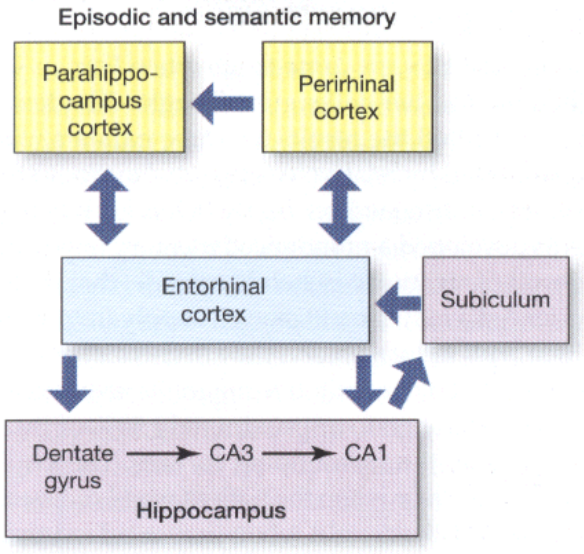


**Figure 17.7.2-1** A further expansion of the top level schematic of the CNS EXPAND around the hippocampal formation. xxx page 256 & 273 See text. From Rudy, 2008.

- - - -

Rudy adopted a figure from Eichenbaum, 2000, and expanded it, **Figure 17.7.2-2**. The introduction to the Eichenbaum paper notes, "Our everyday, conscious memories are not a passive or disconnected collection of images and associations. Rather, we create an intricate network of images and associations, constituting a

record of our personal experiences that is continuously updated through an active organization of new information within the context of previous experience. Recollection is similarly recreative, and the course of remembering is therefore determined by the nature of our memory organization. This type of memory is called 'declarative memory', and is therefore a multifaceted process involving a synthesis of EPISODIC REPRESENTATIONS with our framework of general SEMANTIC KNOWLEDGE that mediates our capacity for recollection. In this review, I will summarize recent progress in characterizing a functional circuit diagram for the brain system that
mediates declarative memory." [xxx add more here, including "However, it is now clear that there are several memory systems in the brain, of which the hippocampal system is only one citation 9 ] [XXX FIGURE 1 is clearer than Rudy relative to the right side ].

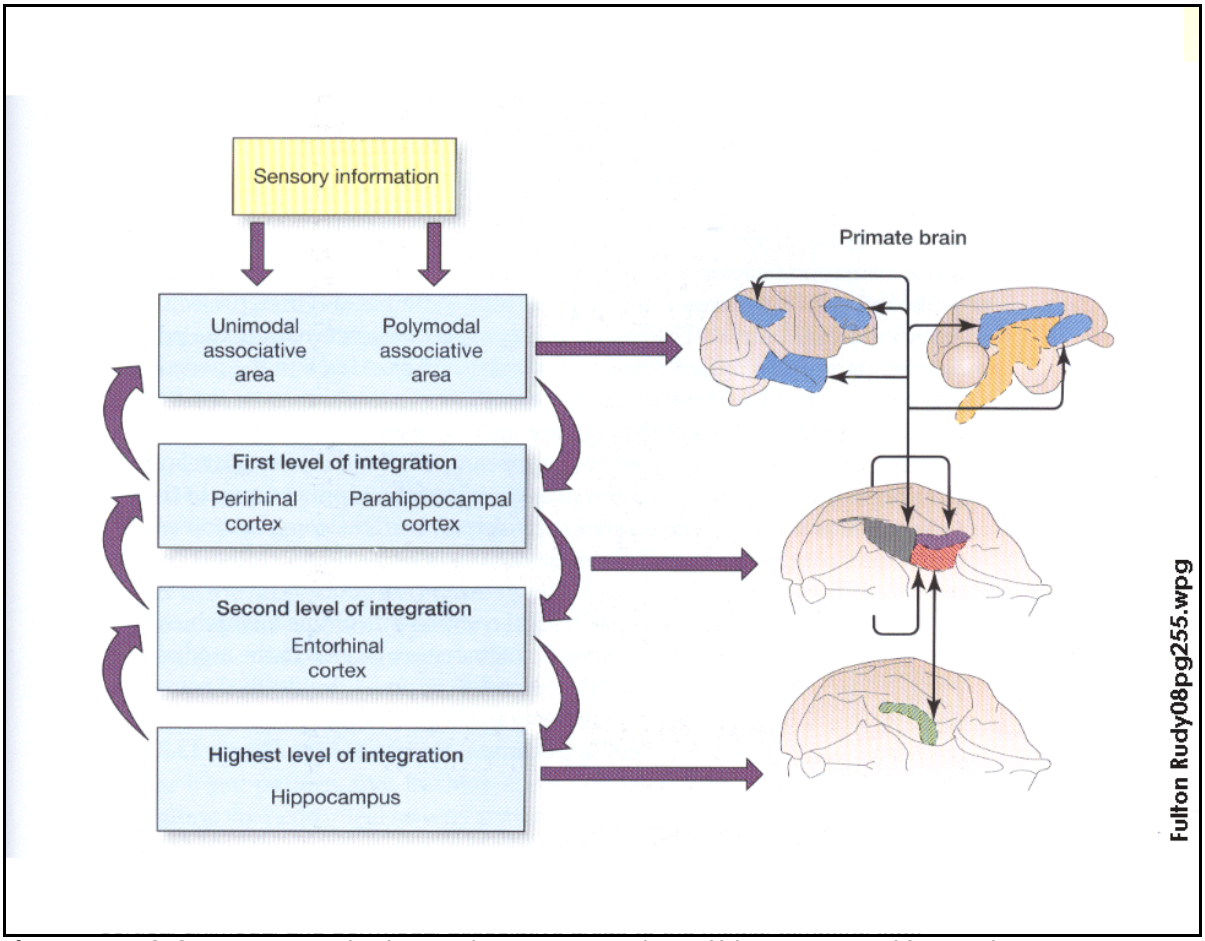


**Figure 17.7.2-2** Conceptual schematic representation of hippocampal formation PRELIMINARY ADD. The dashed border at lower right indicates the entity is buried within the cerebral cortex. From Rudy, 2008.

- - - -

[xxx expand on page 42 of Eichenbaum relating to procedural memory as opposed to semantic and episodic memory. Eichebbaum appears to demark procedural (non-declarative) memory from declarative memory (episodic, semantic and probably numeric).

## 17.7.2.4 The intriguing morphology of the dentate gyrus

The undulations in the inner surface of the dentate gyrus facing the xxx is intriguing because of its potential

analogy. The number of undulations, particularly if it is relatively constant among closely related species might indicate the number of bits in the indexing word (byte) used to store and recall memories. Alternately, the number of undulations might be tied to the number of segments in the total byte associated with the indexing code. Until more information about the indexing code is acquired, little can be said. More research and/or a broader literature search is needed in this area.

### 17.7.3 The best current understanding of database organization-- Index Theory

Of the theories of database organization applicable to stage 5C, at least with regard to the hippocampal formation, is the "Indexing Theory of Episodic Memory" based on the earlier and more generic Indexing "Theory of hippocampal memory" associated with Marr[100] (1971).

Since it is generally assumed that the hippocampus does not actually store any information, and its morphology and histology appear to favor an addressing role, the indexing theory should probably be expanded to include all declaratory and non-declaratory memory. As a result, the following discussion will be related to **an** "Indexing Theory of Memory" within the CNS.

Rudy reviewed the published record supporting the indexing theory. A short coming of the Indexing Theory of Episodic Memory was its limitation to only a portion of declaratory memory. Squire, Cohen & Nadel proposed a modified theory[101], "The Standard Model of System Consolidation" in 1984).

After debate within the community, Nadel & Muscovitch[102] proposed a new theory called Multiple Trace Theory in 1997. This theory asserted that

• Regardless of its age, an episodic memory always requires the hippocampus for retrieval.

• The initial episodic memory trace consists of the patterns of neocortical activity bound together by neurons in the hippocampal formation that serve as an index.

• Each time a memory trace is reactivated, a new index is established to the original neocortical pattern of activity and to other, new patterns of activity that are present. This results in multiple traces that share information with the original trace.

• Older memories are reactivated more often than newer memories and thus have more copies or indices distributed throughout the hippocampus than do new memories.

[xxx expand ]

- - - -

This work proposes a broader based version of the Standard Model incorporating both multiple traces and indexing (**Section 17.7.4**). However, the traces involved are different and the indexing mechanism is broadened.

---

[100]Marr, D. (1971) Simple memory: a theory for archicortex *Phil Trans Royal Soc London Series B* vol 262, pp 23-81

[101]Squire, L. Cohen, N. & Nadel, L. (1984) The medial temporal region and memory consolidation: a new hypothesis. *In* Weingartner, H. & Parker, E. *eds* Memory Consolidation Hillsdale, NJ: Erlbaum & Assoc. pp 185-210

[102]Nadel, L. & Moscovitch, M. (1997) Memory consolidation, retrograde amnesia and the hippocampal complex *Cur Opinion Neurobiol* vol 7, pp 217-227

### 17.7.3.1 The features of a database

The importance of careful database design before enterring any data into it is widely stressed. In the neural database(s), the design has already been determined. As a result, investigators are specifically performing a forensic analysis attempting to define the features previously built into the database design. Searching Google for "types of database," will surface about ten types of databases optimized for different purposes. The dataversity.net has provide a useful introductory discussion of database types[103]. The most commonly used databases are relational database management systems. RDMS, also known as a structured query language. Their range of application is very wide. Because of their wide usage, their terminology has become standardized. The dataversity website has including a set of pro's and con's for Relational/SQL and Non-Relational/NOSQL versions.

There are also special databases for addressing graphic and multi-dimensional data. However, at this time no investigator has reported discovering the database structure used in the neural system, it is premature to discuss the specific database employed. In the vast majority of man-made databases, a rectilinear framework of rows and columns is use to hold the data. However, there is a vast array of Riemann Transforms that can be used to create non orthogonal frameworks, such as the one used in the hearing modality of biology.

> The Tritone Paradox of human hearing can only be explained by recognizing the Riemann Transform used in primate hearing (**Section 8.4.7.3** in **PBH**).

- - -

Eichenbaum (2000) presented an excellent paper on the attributes of the memory system discernable when only its behavioral aspects can be documented.

- - - -

## 17.7.4 Proposed broader Standard Model of Memory Creation, Storage & Recall

Most of the analyses in this work were developed from the non-psychological database, until the questions of learning and memory became relevant. At that point a concerted effort was undertaken to understand the psychophysical aspects of the CNS, including both cognition and learning based on logic **and** cognition and learning based on emotion. The portion based on logic employed elements of the striatum and pallidum to mediate the learning and recall processes whereas the portion based on emotion employed elements of the hippocampal formation to mediate learning and recall. Because of the flexibility involved in using mathematic, semantic & mnemonic stimuli along with episodic memory in the category of declaratory memory, these categories of memory have been associated with the hippocampal formation, As a result both emotion-based and non-emotion based elements of cognition have been mixed in the discussion of the hippocampal formation within the psychology community of neurobiology.

Based on the entire Learning and Memory formation, storage and recall addressed with respect to non-declaratory, declaratory and Phylogenic memory in this work, a new theory is proposed that encompasses the entire realm of Memory (see figures and text in **Section 17.1.2**) as well as a broader view based on neuroscience.

> The new theory recognizes the fact that the results of emotion related cognition does not result in the same degree of memory formation as most other types of memory.
>
> The role of the cerebellum, which has been largely ignored with respect to memory in the academic literature is recognized as the principle source of all memory oriented activity. Its size in neurons is taken as equal to all other neurons in the CNS ***combined***.

### 17.7.4.1 Basis of the proposed Standard Model of all biological memory

Rudy has provided a good discussion of learning and memory based primarily on the fundamentals each

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[103](2017) http://www.dataversity.net/review-pros-cons-different-databases-relational-versus-non-relational/

author highlighted relative to his stated theory. The location of these theories in his text are indicated in **Section 17.2.5** of this work. The views were invariably from the neurobiology perspective. He has boiled each of these discussions down into a set of bulleted points characterizing the individual theory. Many of the characteristics listed are not necessarily as specific as desired in this work. This subsection will address each of these fundamental bulleted points with the intent of providing a more specific, and/or more comprehensive description.

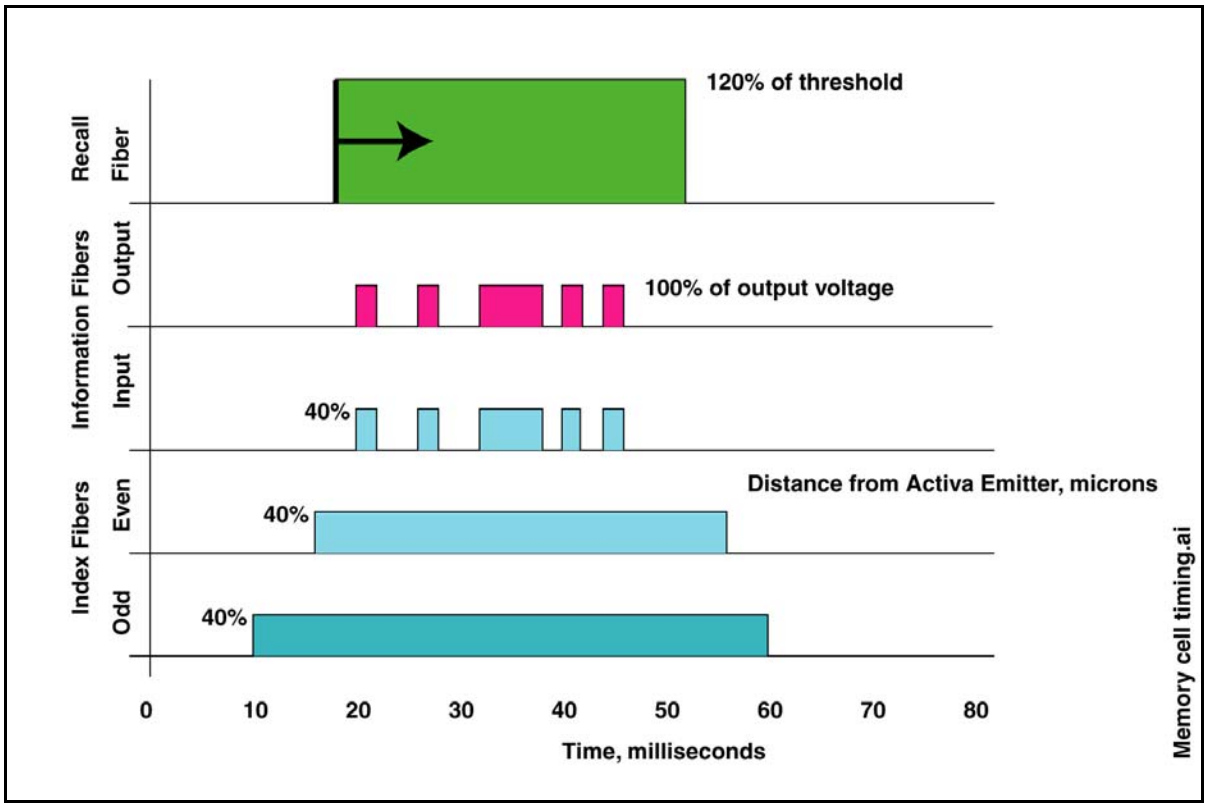


**Figure 17.7.4-1** Candidate memory cell timing diagram ADD. See text for details of operation. The diagram applies to the writing, storage and accessing a particular record stored on a specific xxx neuron, particularly of the cerebellum.

### 17.7.4.1.1 Indexing scenarios analogous to the telephone network

Most people are unaware of the total scope of the architecture of the switched telephone network. The telephone switching architecture developed in the 1940's was carefully structured to meet the needs of the entire World for more than 50 years. It included reserved blocks for growth, for maintainence, etc. The architecture was designed to include up to 16 decimal digits as found on some telephones, particularly those used within the US military, 0 through 9 and the letters A through F. It was also designed to allow for up to 16 decimal digit addressing. Thus a typical complete telephone index might look like,

| | | |
|---|---|---|
| First index | 0–F | Wide area (typically a continent) |
| second index | 0–F | Country code (two digit index if desired) |
| third index | 0–F | Area code within a country (3 or 2 digit index based on above) |
| fourth index | 0–F | Local exchange (3 digit index) |
| Fifth index | 0–F | Local line (four digit index connecting to an individual telephone) |

Thus a single telephone index might look like the following,

| | |
|---|---|
| 4– | Europe |
| 4,4– | Great Britain or |
| 4,41– | Northern Ireland |
| 4,13A– | Western Scotland |
| 4,13A–55D– | A Glasgow local exchange |
| 4,13A–55D–1212 | A local residence in the Glasgow region of Scotland |

Countries have been provided great flexibility in where they introduce commas and or dashes into their local semantics, but they all ultimately fit into this structure. For instance, dialing 44-28-555-1212 will get you a telephone in or near Belfast Northern Ireland. 58-212-55-1212 will get you a telephone in or near Caracas, Venezuela, South America.

It is likely that the neural memory indexing scheme is similar in architecture to the above architecture. As an example, consider [**Figure 17.1.2-1**] reproduced here with an overlay as **Figure 17.7.4-2** Let non-declaratory memory be designated using the codes 0–4 and declaratory memory be designated using the codes 5–9 in the first indexing position. Reserve for now the digits A–F. The row below these labels in the figure can then be designated by the remaining indexing codes in the first position, or they can proceed to employ the 2nd index code position.

Some systems around the world have been setup to access the World wide telephone network, the "long distance" network, by dialing a prefix to the above codes of 1, 01 or 00. These codes are primarily for local billing purposes.

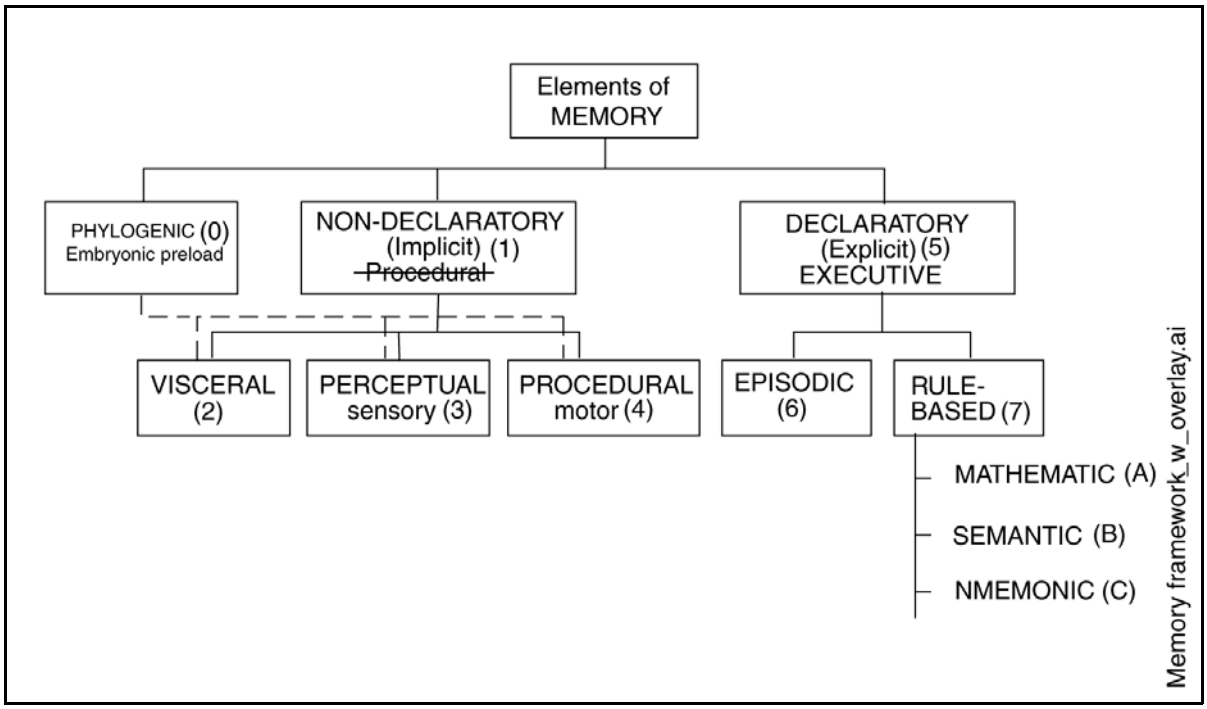


**Figure 17.7.4-2** Example of potential memory architecture ADD. The categories at lower right are liable to expand. See text.

- - - -

Assigning the initial index of (0) to the prenatal (probably read-only) phylogenic memory appears appropriate.

- - - -

Employing additional cross-bar, or parallel fiber-bar switches prior to the switches at the local circuit level, as is commonly done in telephony, is achieved with minimum complications.

- - - -

Using the basket cell axons contacting the peripheral (poditic) inputs to one or more Purkinje neurons achieves *en banc* inhibition of multiple neurons associated with a given pseudo-topical region of the cerebellum. En banc inhibition can affect a large segment of a single folium or a group of folia as suggested in [**Figure 10.2.4-4**].

## 17.7.4.2 Fundamentals underpinning the proposed Standard Model of Biological Memory

In describing the fundamentals associated with the Standard Model of Biological Memory, approximately 30 fundamentals have been defined that support the operation of the CNS. These fundamentals include,

• There are at least three types of memory in the case of the higher animals, short-term memory, long-term memory and working memory.

• To accommodate the requirements of stage 5 cognition, the learning process involves multiple temporally sequential memory traces.

• To accommodate declaratory, non-declaratory and phylogenic memory, a variety of memory traces can be identified with respect to time, type of stimulus and subject activity.

• To accommodate the learning process as well as memory formation, the cerebellum is organized as a relational database management system, RDMS. The RDMS employs an indexing system similar to that used in similar man-made systems.

• The words (bytes) used in the indexing system may be larger than that used within any sensory, cognitive, instruction or command record in order to accommodate potentially significant amounts of metadata.

• The cerebellum stores the signal patterns brought to its purview as individual records and groups of records supporting a specific record in totally abstract form.

• The records stored in the cerebellum may incorporate multiple records, related by time period, spatial relationship or other features of significance.

• The records initially stored in the cerebellum are described as short-term memories. For a variety of reasons, these records are improved in quality over a period of time before they are adjudged long-term memories.

• Records relating to pain, rage, and other emotional conditions are not routinely delivered to the storage system via the hippocampal formation for purposes of short-term or long-term storage.

• Long term memories stored in the memory system are routinely refreshed (a.k.a. consolidated) through their being called into working memory.

•When totally abstract records stored in the cerebellum are recalled by the control circuits of the thalamic reticular nucleus, TRN, they may be reconstituted first as the best available analog representation of the stored record.

• The records recalled by the TRN are placed in “working memory” for comparison with the current representation of the environment.

• The comparison of two records placed in working memory may employ “fuzzy logic” or a truncated recalled

record.

• To accommodate the learning process, as well as the recall and comparison involving current representations of the environment *and* stored earlier representations, the memory traces may represent literal (environmento-topic) representations as well as totally abstract representations of a given record.

• When the comparison between a current representation and previously stored records of similar representations fails to satisfy a quality standard, the current representation may be passed to the appropriate stage 5 cognition mechanism to extract a new abstract record describing that representation.

• When, the current and recalled stored memory are found to match adequately, the abstract form of the record may be flagged in the metadata to indicate it can be used in the future to implement a reflex path via the circuits associated with the cerebellum (labeled the $R_C$ or $R_{S-P}$ paths in the proposed schematic diagram) that causes the subject to react faster to threats in the future.

•The reduction in response time to a major external threatis a major purpose of practice as a behavioral learning tool.

• Following the extraction of a new abstraction describing a new representation, that abstract record will be passed back to the storage mechanisms of the CNS for storage within the appropriate database of the cerebellum.

• Newly stored abstract records may be truncated for optimal storage.

• When two records stored in the cerebellum are similar, their indices may be linked, or contain within each index a reference to the other index.

• When a new abstract record delivered to the storage mechanism is judged by the stage 5 cognition process as an update of a previous stored record, the previous record can be replaced by an updated abstract record.

• To accommodate the declaratory, non-declaratory and other memory stores, the cerebellum is subdivided according to the task(s) it is responsible for.

• To accommodate rapid search of the various databases of the CNS, a type of binary search procedure is used under the control of the indexing circuits.

• When an abstract *instruction* is issued by the engines of stage 5 cognition to the efferent, stage 6, engines of the CNS, these instructions, are first expanded into a set of literal *commands* for delivery to the musculo-skeletal system and/or the hormonal system, and potentially the visceral system.

- - - -

To understand the role of all of the above "fundamentals," it may be best to prepare a state diagram, consisting of the proposed schematic of the CNS in **Section 17.7** and the above list of fundamentals**.** ***The graphic representing the state diagram will not be small and probably should be drawn on a 3 foot wide roll of paper.***

### 17.7.4.3 xxx A concise, abbreviated, statement of the Standard Model of Memory EMPTY

### 17.7.5 Candidate Memory Cell for biological memory applications

The candidate memory cell of stage 5 to be described in this section depends on various signals from other engines of the CNS, particularly the brain stem. **Figure 17.7.5-1** describes the general situation involved.

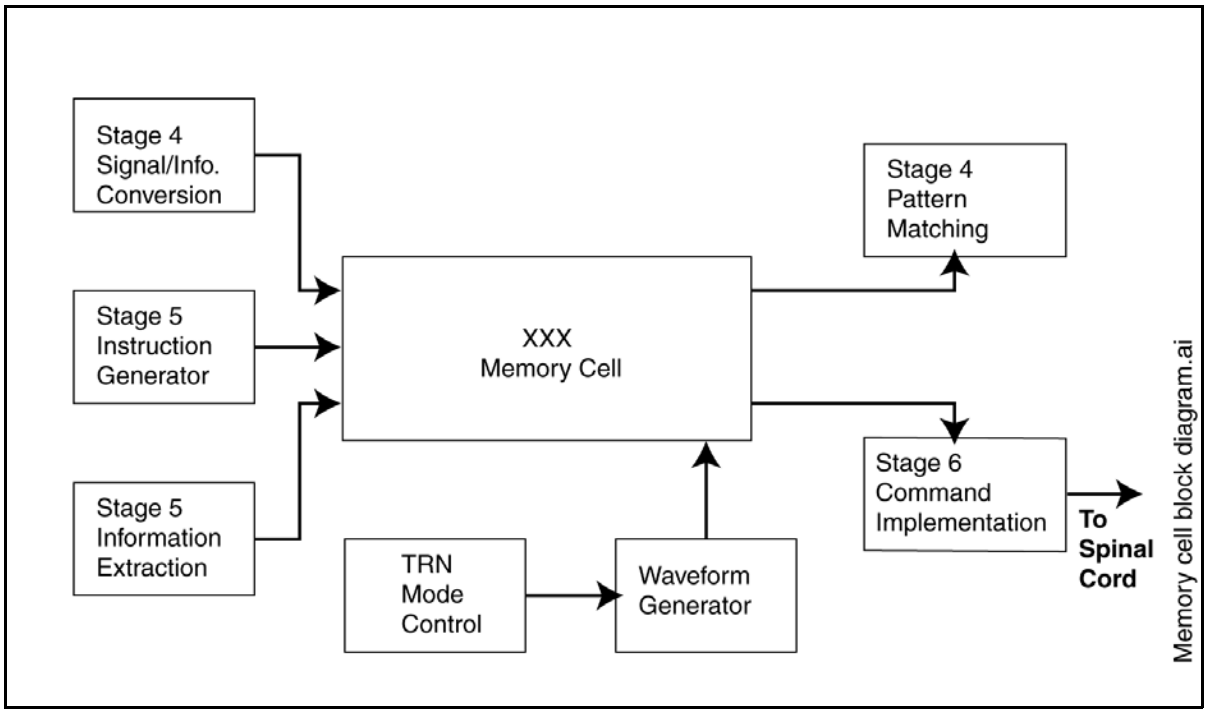


**Figure 17.7.5-1** Block diagram of memory activities within the cerebellum ADD EMPTY. See text.

## 17.7.5.1 Memory cell schematic diagram EMPTY

**Figure 17.7.5-2** shows the schematic of the candidate memory cell and accompanying climbing fiber after decoding at the xxx.

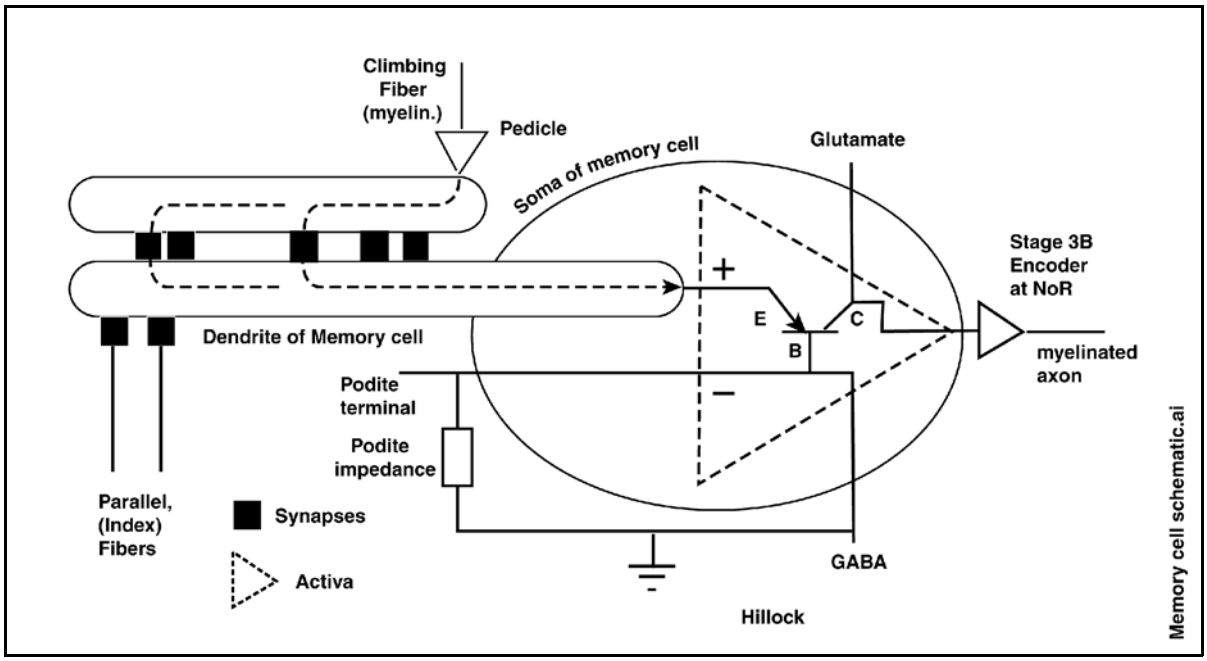


**Figure 17.7.5-2** Schematic diagram of memory recording in the cerebellum. Glutamate & GABA are molecules providing the electrical energy to the neuron. The myelinated axon on the right can extend to several terminals as shown in the block diagram. The podite terminal is shown as open, because there are a variety of options available. See text.

- - - -

Desclin noted, "Branching of climbing fibers occurred fairly frequently at the level of the infra-ganglionic plexus. In favorable cases both branches from the same climbing fiber were seen reaching distinct Purkinje cells lying 12-14 cells apart from each other. Branching could also sometimes be observed in the deeper zones of the granular layer, but we did not succeed in tracing them far enough to see both branches reach the molecular layer.

> The grouping of 12-14 Purkinje cells could support a word serial/bit parallel signaling concept employing 12-14 bit words. This is entirely possible considering man-made computers are now using 32–64 bit and wider words.

- - - -

## 17.7.5.2 Memory cell timing diagram

**Figure 17.7.5-3** shows a candidate memory cell timing diagram that can be used with the above candidate memory cell to explain how memories are written into such a cell, stored and accessed. Access can be for purposes associated with,

• afferent stage 4 operations, pattern matching to abstract information about the external or internal environment,

• efferent stage 5/6 operations, transforming stage 5 instructions to stage 6 commands,
• learning, including memory record update,
• declaratory memory recall, a stage 5/6 operation.

One mechanism on which these operations depends remains unknown but is now of considerable interest, ***how are synapses physically formed at a given location(s) along the climbing fiber and between the climbing fiber and one of the dendrites of the yyy xxx neuron?*** The distance between the synapse and the stage 3B decoder of the climbing fiber is critically important when added to the distance between the synapse and the emitter input of the Activa within the yyy neuron since the signal travel at conductive (diffusion) rates over these distances.

The engines generating the waveforms in the following discussion will be described in other sections of this chapter [xxx ].

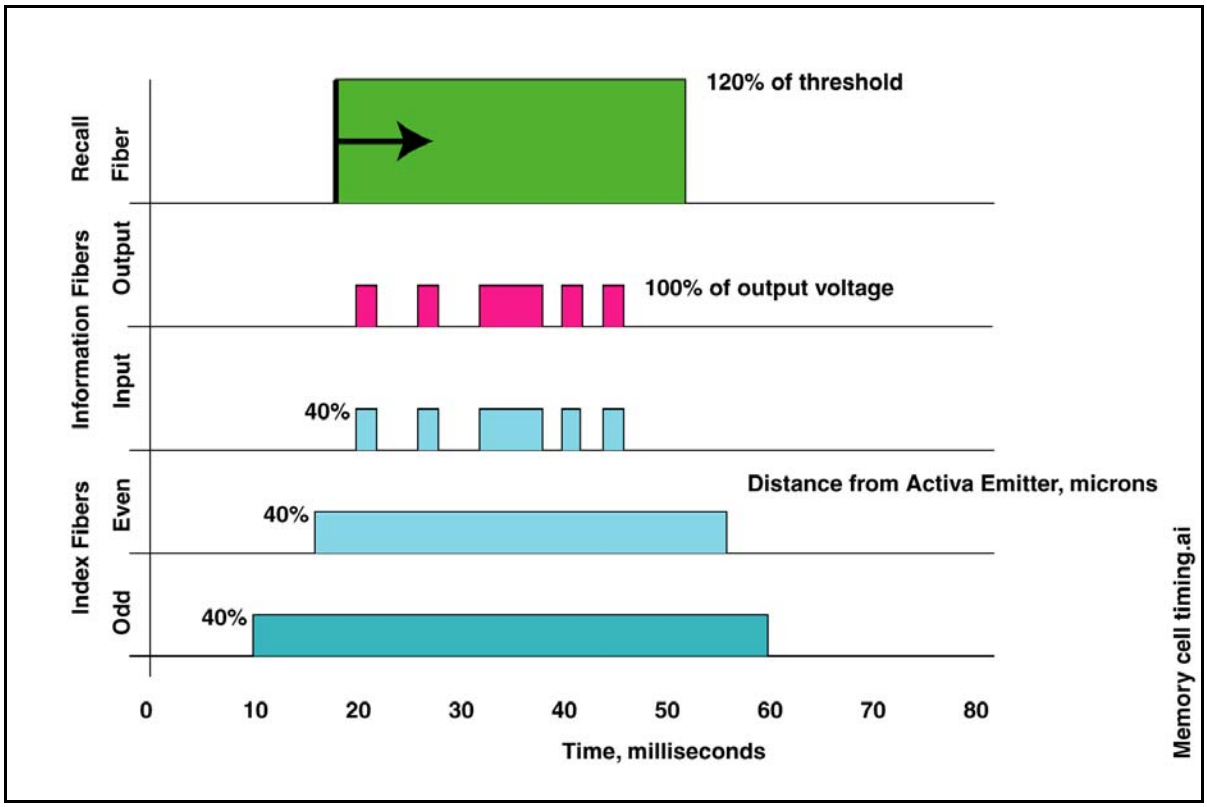


**Figure 17.7.5-3** Candidate memory cell timing diagram ADD. See text for details of operation. The diagram applies to the writing, storage and accessing a particular record stored on a specific xxx neuron, particularly of the cerebellum.

### 17.7.5.2.1 The writing of a memory record

### 17.7.5.3 xxx EMPTY

### 17.7.5.4 xxx EMPTY

## 17.7.6 Candidate memory switching process

Based on the previous discussions of switching architectures, there are a wide variety of these conceptual architectures. **Figure 17.7.6-1** presents one of these a potential block diagram of a memory switching process primarily for discussion. It appears capable of supporting both initial memory storage and memory the memory selection and recall process.

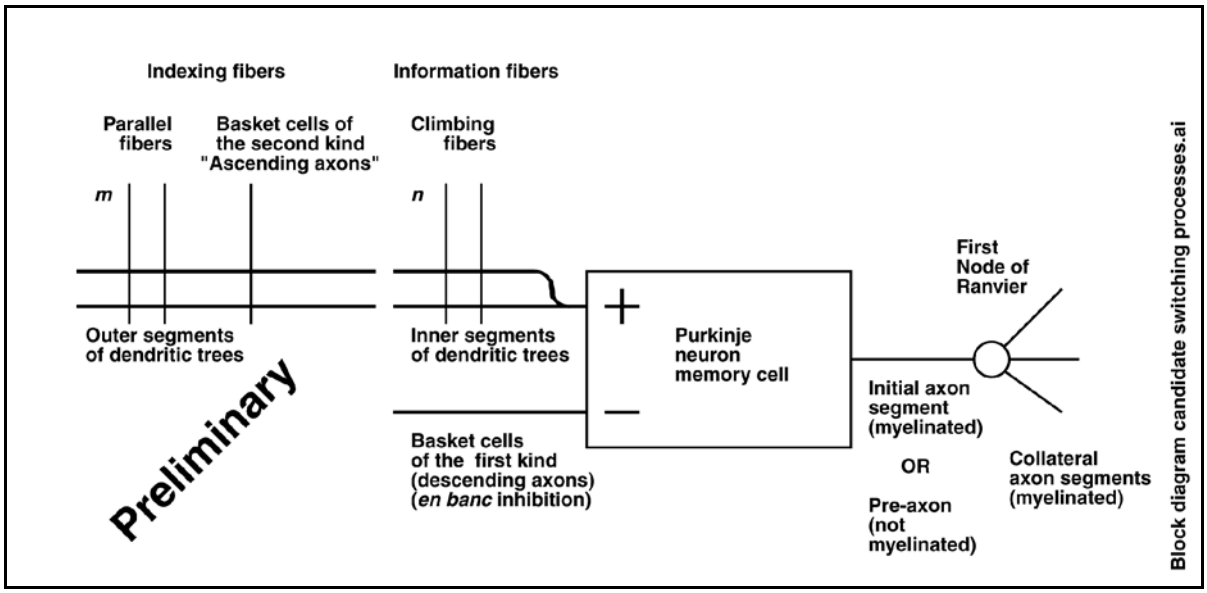


**Figure 17.7.6-1** Candidate memory system switching process ADD used for both initial memory storage and memory recall purposes.

All of the elements described in this figure have been discussed and/or described in earlier sections of this Chapter. The assignment of specific types of indexing fibers are totally arbitrary at this time. The literature is not sufficiently descriptive to associate specific parallel fibers or basket cells of a particular kind to the indexing function related to a specific folia or Purkinje neuron. Similarly, the descriptions of climbing fibers in the literature are not sufficient to show where they arise in the pseudo-topical areas of the cerebellar cortex.

- - - -

While the climbing fibers have been traced to the xxx, they have not been traced farther to specific locations within the xxx of the cerebellum.

[xxx add more background for this figure ]
- - - -

Braitenberg & Atwood have studied various sheets of neural tissue with a specific paper relating to the sheets within the folia of the cerebellum[104]. [xxx find a home and expand on this paper ]

- - - -

### 17.7.6.1 Indexing strategies

[104]Braitenberg, V. and Atwood, R. (1958), Morphological observations on the cerebellar cortex. *J Comp Neurol*, vol 109, pp 1–33 doi:10.1002/cne.901090102

As noted in the above figure, there are at least three sets of indexing elements,
1. the parallel fibers (axons) created by the granule cells
2. the ascending fibers (axons) arising from a type of basket cell
3. the descending fibers (axons) arising from a type of basket cell.

As noted in Eccles et al., the label of basket cell is almost generic. They take pains to differentiate the basket cells from those labeled Golgi cells in the xxx layer of a folium.

-_ - - -

As demonstrated in the above material, the parallel fibers are present in great numbers within the molecular layer of each folium. They are also carefully aligned with the longitudinal axis of each folium. While many hundred thousands of parallel fibers may intersect the fan of an individual Purkinje neuron, only a smaller number, m in the figure actually synapse with an individual Purkinje neuron. M is a poorly defined number in the literature, with a large deviation associated with the average value.

As noted In Eccles et al. (page 93), Szentagothai postulated in 1963 and 1965a, that the crossing-over synapses on the dendritic spines are excitatory and that the basket cell synapses are inhibitory, so giving a wide zone of inhibition on each side of the excited zone on-beam." This work does not support any inhibitory synapse that is not associated with the poditic terminals of the Purkinje neuron located around its basilar periphery. On page 95, Eccles et al. note, "The Purkinje cell baskets are a synaptic system of almost unique architectural design. An EM analysis shows that there is no contact between the descending basket axon collaterals and the upper part of the Purkinje cell body, which is sealed from its environment by an envelope of the Bergmann-glia." Their figure 56, shows the basket axon collateral synapsing with the lower part of the Purkinje neuron in the area where the hillock would be found morphologically and where the base of the Activa is found. synapses between these descending basket axon collaterals in this area would be expected to be subtractive **or** inhibiting depending on whether the region is operating in the analog or pulse mode. The figure also supports the concept of a preaxon in this location. This location is shown as the base region of the Activa on the right frame of [**Figure 17.6.1-6**]. Pages 93-96 of Eccles et al. provides more discussion of the descending basket cell axons.

As noted by Eccles et al. (page 94), the basket cell type apparently involved in indexing is "remarkable both with respect to its characteristic course, which is strictly parallel to the surface and with the transverse plane of the folium and in terms of its highly specific ramification." The descending axons of a single basket cell of this type can contact multiple Purkinje neurons in a longitudinal span of at least

### 17.7.6.2 Information storage strategies EMPTY

## 17.7.6.xxx Analyses of Szentagothai paper of 1965a

The Szentagothai paper of 1965 is an extremely important paper in the context of this work and the symbiotic relationship between the two cannot be overlooked. A key problem in the 1965 paper is stated on page 93 of Eccles et al., In an attempt to give a meaningful interpretation of this pattern of action on Purkinje cells, Szentagothai (1963, 1965a) postulated that the crossing over synapses on the dendritic spines are excitatory and that the basket cell synapses are inhibitory, so giving a wide zone of inhibition on each side of the excited zone on-beam." This postulate is aligned with the chemical theory of the neuron commonly accepted in that time period. However, it led to situations that Szentagothai could not explain, how for instance the axon collaterals of a single neuron could be both excitatory and inhibitory. In discussing inhibition by basket axons synapsing with the soma of a Purkinje neuron near its lower periphery, Szentagothai noted, "It was not clear, however, whether the influence exercised by basket axons upon Purkinje neurons is excitatory or inhibitory. Although, as I have been pointing out, the structure does 'make much more sense' if this influence is inhibitory, this is no proof."

By changing from the position that presynaptic collaterals of the same axon could be both excitatory and inhibitory, to the concept that the post synaptic neuron had a differential input structure, with the apical dendritic structure always excitatory, signal non-inverting, and the poditic structure always inhibitory, signal inverting, his challenge was resolved and his task becomes much simpler.

In the discussion, Eccles noted, “These results are precisely explicable by the two actions of the parallel fibers; direct excitation of the Purkinje cells by axo-dendritic synapses, and disynaptic inhibition my mediation of the basket cells that ar directly excited by parallel fibers and than in turn send axons transverely across the folium to inhibit Purkinje cells by axo-somatic synapses in a zone far beyond the excited Purkinje cells.”

The paper read by a leading histologist of his day in the presence of Sir John Eccles, a dominant physiologist of his era, appears to have led to the 1967 book by Eccles, Ito & Szentagothai, abbreviated at many points above as Eccles et al. As frequently necessary, that book condensed much of the material in the 1965 paper. The 1965a paper provides the additional details needed to support this work. The discussion at the end of the reading of the 1965 paper is nearly as important as the text itself.

The paper relies upon a variation of the degeneration methods typically used in histology. In this case, he caused the degeneration of large number of neurons that left other neurons clearly identifiable as “persisting elements.” Of course, this worked best when there were only a few types of neurons present in a given tissue sample, and an adequate nutrient supply remained available.

The paper addresses a variety of situations related to the cerebral cortex before focusing on the cerebellar cortex. In the opening sentence of that material, he significantly contradicts himself in the interests of social acceptance, “. . .neuronal connexions were already correctly understood by the neuro-histologists of the classical era around 1890.” Signal paths, yes; but the function of the connexions, no!!

He provides valuable backup for the physical range of the fibers found within the cerebellum and summarized in Eccles et al. Similarly, for the number of synapses in a given region. He also discusses the concept of divergence and convergence more explicitly in the paper than in Eccle et al. His figure 19 brings more clarity to [**Figure 17.6.1-5**]. He stresses the orthogonality of the basket neuron axons and parallel fibers. They are under limited circumstances the direct analog with a man-made cross-bar switch.

Page 12 enters an area of less clarity, accompanied by a large number of electron microscope images trying to differentiate between a large number of ancillary neuron types surrounding, and mediating the signaling elements that contact the Purkinje neurons.

On page 20, Szentagothai introduces the subject of integrative units within the cerebellum by noting, “that there are no anatomically predetermined units as in some parts of the cerebral cortex, . . .” This statement is arguably inadequate. He introduces the term “these speculations” into the text at this point. He does confirm, “that most of the surface of the Purkinje cell soma and especially of the main dendrites is completely sealed from the environment by a layer of glial tissue. The basket neuron terminals have access only to the lowest part of the cell body around the axon hillock.”

On page 21, he transitions into a discussion of the more complex synapses, identified as either glomeruli or cruciform connexions. He noted Cajol used the term glomeruli in a similar context as early as 1911. He concludes in 1965, “a closer investigation of the glomerular synapse appears to be worth while. Speaking of the Golgi axons in the glomerular synapse, “We do not know as yet, whether this influence is facilitatory or inhibitory, but in any case a feedback, either positive or negative, is exercised mainly from a longitudinal strip or funiculus of simultaneously active parallel fibers upon the very synapses through with ths activity has been set up.”

Szentagothai does not discuss the potential indexing function associated with the neurons supporting the Purkinje neurons in their role as primary memory units.

## 17.7.7 Learning & precision movement based on the cerebellum

While the functioning of the cerebellum as the location of the principle site of memory storage, the location of the engines controlling the switching involved in memory storage, memory recall and memory updating is still speculative. From a traffic perspective, it appears that the interposed nuclei located within the central area of “white matter” of each folium and the overall cerebellum are the engines associated with these functions. Thus signals to and from the cerebellum and the pons are routed through these engines. They form a “local

minibrain," not unlike that found in the auditory modality and the cardiological modality. Signals relayed through the pons extend upward through the thalamic reticular nucleus, TRN, to the remainder of the CNS and external sensory modalities of the cranium; and downward through the spinal chord to the remainder of the PNS and via the vagus nerve to the other internal sensory modalities.

Much of the discussion related to the function of different neural paths are based on the premise that there are excitatory and inhibitory axons (although no means of distinguishing them is presented). This makes most of the discussion in chapters XI and XII of Eccles et al. incompatible with the situation according to the Electrolytic Theory of the Neuron. This Theory associates the apical dendritic tree of a neuron with the non-inverting or excitatory signal path relative to the axon of that neuron. It associates the poditic input terminals located along the periphery of the base of the neuron with the inverting or inhibitory signal path relative to the axon of that neuron. This Electrolytic Theory of the Neuron leads to an interpretation of neuron operations that is compatible with the signal paths of Eccles et al. but not with the signal processing associated with those paths.

The following material is based on a reinterpretation of the Eccles et al. (1967) text and the academic literature condensed into that volume. An equally massive volume (930 pages) to that of Eccles et al. was published in 1969 that is worthy of review[105]. It explores the role of the cerebellum in a wide variety of species. It is primarily an atlas of electron micrographs with introductory remarks. It does provide discussions of the neuron types found in the cerebellum. [xxx where are words relating to this volume? ]

### 17.7.7.1 Cerebellum topographies related to memory switching

Chapter XI and XII of Eccles et al. (1967) provide a contemporary review of the topography of the cerebellum and its principle neural types. Pages 195-197 provide a good overview of the design problem of packing maximum amount of memory in a minimum volume while accommodating the required indexing axons and central control functions. They reiterate the fundamental memory cell volume as consisting of two parts, the first represented by only the dendritic fan of a Purkinje neuron, 300 x 225 x 6 microns. The second by only the soma of the Purkinje neuron with a transverse diameter of 30–35 microns and an axial diameter of 50–70 microns. The soma are staggered in the transverse dimension and spaced at approximately 50 microns. The 2 microns spacing between the dendritic fans are occupied by a variety of dendrites associated with the indexing and sensing neurons.

**Figure 17.7.7-1** summarizes the topography of the cerebellum near the surface of a folium as well as possible in a limited space.

[105]Llinas, R. ed. (1969) Neurobiology of cerebellar evolution and development. Chicago, Il: American Medical Association

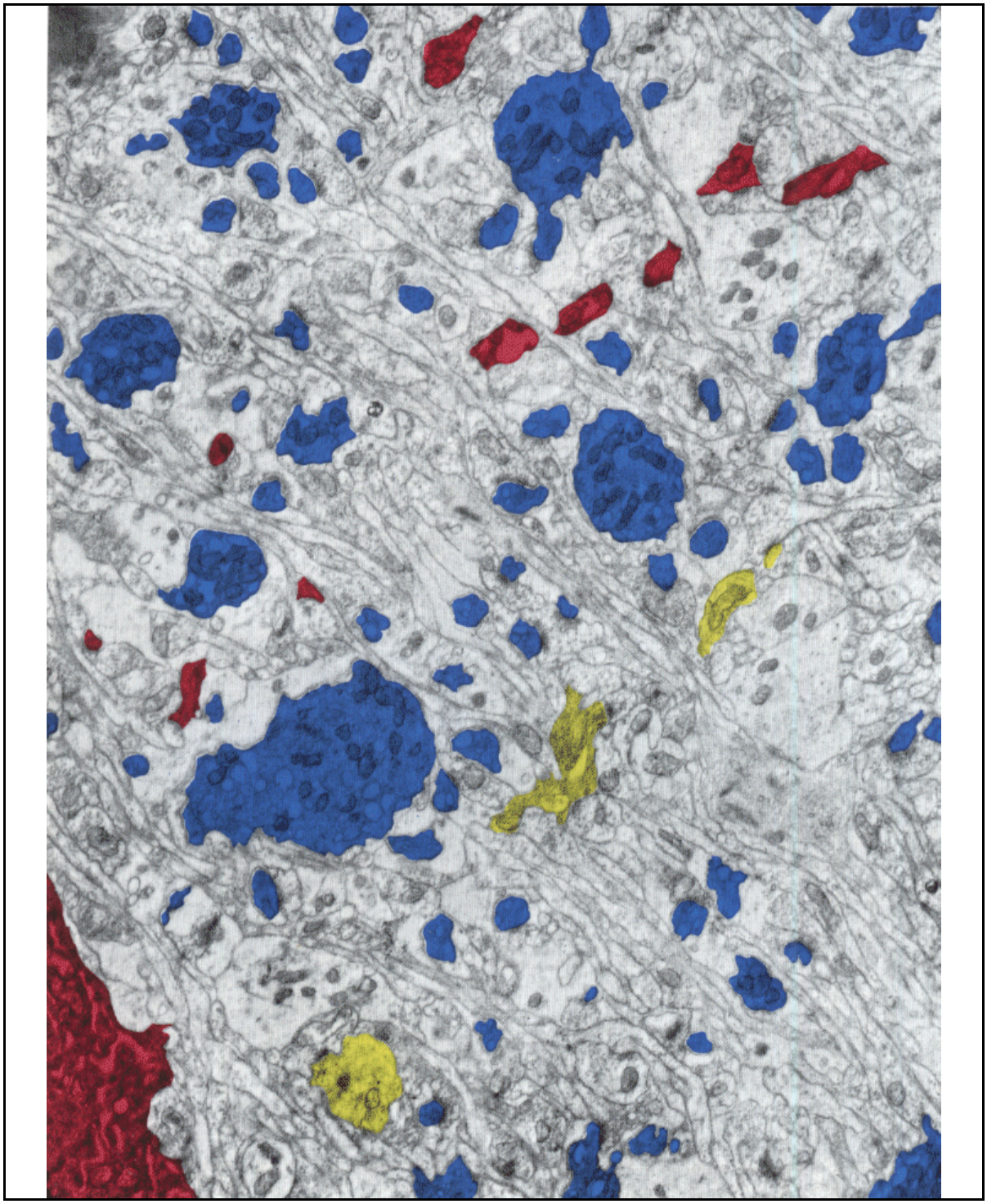

**Figure 17.7.7-1** Tangential—surface parallel—section of the molecular layer in the cat. Various kinds of dendrites have been indicated in colors. Purkinje dendrites and their spines in blue, basket dendrites in red (basket cell body at lower left corner) and probably Golgi dendrites in yellow. Arrangement of dendrites in alternating transversal sheets—here running from right above to left below —can be well recognized. Parallel fibers are left uncolored and are seen to run in bundles in the longitudinal direction of the folium—here from left above to right below. From Eccles et al., 1967.

### 17.7.7.2 The role of the interposed nuclei of the cerebellum

Eccles et al. (1967) do not provide significant attention to the interposed nuclei (pages 268-288). On page 262, they note, "A general survey of the nuclear efferents of the cerebellum is given by the summarizing diagrams of Jansen & Brodal (1954 Fig.71; 1958 Fig. 187)." After a few other remarks, they go on, "Every thing known then has been so well documented by Jansen and Brodal (1954[106,107], 1958) that nothing could be added to these masterpieces of functional anatomical analysis." A contemporary review of Jansen & Brodal by von Bonin provided a more balanced discussion. The text is dominated by long descriptions largely devoid of any tractology. Little information related to the interposed nuclei was recognizable in these descriptions. A major portion of the Jansen & Brodal work involved the fin-whale. Much of the terminology appears to be that of zoology. Von Bonin provided a translation into recent biological terminology[108]. He then synopsised the book better than this analyst could. See **Section 17.7.7.2.1** and **Section 17.7.7.2.2**.

A more recent investigation of the engines of the interposed nuclei, using newer techniques, includes the paper (using rats) by Sharp & Ryan[109]. Other relevant papers (using cats) include Walberg[110]

On page 276, Eccles et al. note, "The inhibitory control by the Purkinje cell axons presupposes that there is a tonic excitatory state in the subcortical nuclei, otherwise, there is no background to be depressed by the inhibitory action of the corticofugal impulses from the Purkinje cells." This presupposition is counter to the Electrolytic Theory of the Neuron presented here. With respect to afferent signals, primarily from the sensory modalities, the purpose of the cerebellum ***is not to truncate or perform some fuzzy logic*** on the sensory signals ***but to store the very essence of those signals*** and metadata associated with those essences. Similarly with respect to efferent signals, the primary purpose of the cerebellum ***is not to suppress*** portions of the instructions received from the stage 5A and 5B cognition engines ***but to embellish or augment*** these instructions as they are expanded into commands required to coordinate a wider range of targets (predominantly muscles) in order to smooth observed behavior. The extraction of the essence of stage 4 afferent sensory signals and the embellishment of efferent stage 6 commands are complimentary and even more important are complimentary across the conceptual declaratory and non-declaratory boundaries described in various contexts. This sharing is illustrated by the engines associated with stage 4b and 6b in **Section 17.7** where the discussions are based on similar figures in other chapters of this work (**Section 4.6.3**).

Teasing apart the engines of the interposed nuclei in order to determine their principle roles is the goal of this section. However, von Bonin has provided a good summary of that information.

### 17.7.7.2.1 The afferent cerebellar circuits of the interposed nuclei

---

[106]Jansen, J.(1954) Efferent cerebellar connections *In* Jansen, J. & Brodal, A. *eds*. Aspects of cerebellar anatomy, Oslo, Johan Grundt Tanum pp 189-248 QL 937. J3 A review of this book by von Bonin is quite informative, http://onlinelibrary.wiley.com/doi/10.1002/cne.901010311/full See below.

[107]Brodal, A. (1954) Afferent cerebellar connections *In* Jansen, J. & Brodal, A. *eds*. Aspects of cerebellar anatomy, Oslo, Johan Grundt Tanum pp 82-188

[108]Von Bonin, G. (1954) Review of Aspects of Cerebellar Anatomy *J Comp Neurol* vol 101(3), pp 830-834

[109]Sharp, F. & Ryan, A. (1984) Regional ($^{14}$C) 2-deoxyglucose uptake during forelimb movements evoked by rat motor cortex stimulation: Pons, cerebellum, medulla, spinal cord, muscle *J Comp Neurol* vol 224(2), pp 286–306

[110]Walberg, F. (1956) Descending connections to the inferior olive. An experimental study in the cat *J Comp Neurol* vol 104(1), pp 77–173

Von Bonin summarized the work of Brodal cited above. The summary is reproduced here.

> The second chapter, on the afferent connections of the cerebellum is by Brodal. He reviews the dorsal, the ventral, the intermediate spino-cerebellar tract (the last one of which is very weak), the cerebellar afferents from the external cuneate nucleus, which go almost completely to the anterior lobe, the olivo-cerebellar connections, which go to the whole cerebellum and show a definite topological organization. There is an excursus on the spinal afferents to the inferior olive, which makes it clear that they only go to a part of the olive. To resume the main trend, the ponto-cerebellar connections are taken up next, and here again a fairly clear cut topographic organization can be discerned. Then the afferents to the pons are discussed: they come from the cortex, and arise there in all 4 lobes. There are some tecto-pontine fibers, and also some, although not too many, spinopontine-fibers, showing that the pons, too, does not only rely on afferents from higher levels. Then reticulo-cerebellar connections are discussed, among whom the lateral reticular nucleus is treated at greatest length. Then follow the afferents from the perihypoglossal nuclei, the rubro-cerebellar connections, the tecto-cerebellar, trigemino and vestibulo-cerebellar connections, and a short remark on the lateral cervical nucleus, which is present only in some forms but apparently absent in others. *Among those in which it is absent, is man*. It is present in the cat, dog, sheep and whale. No reason for these differences can be given. The projections from the spinal tracts show much less somatotopical organization than the shorter projections from the inferior olive, from the pons, etc. One gets the impression (not mentioned by Brodal) that much of the somatotopical organization is simply a matter of getting there fastest and easiest, and has little to do with the function of the cerebellum. Lashley expressed similar views on several occasions (see e. g. Biological Symposia, vol. VII, p. 301-322.

### 17.7.7.2.2 The efferent cerebellar circuits of the interposed nuclei

Von Bonin summarized the work of Jansen cited above. The summary is reproduced here.

> "In the third chapter, the efferent connections are treated by Jan Jansen. It starts out with a consideration of the connections between the cerebellar cortex and the nuclei of the cerebellum, of which three, the nucleus fastigii, the interpositus and the lateralis are recognized. The last named is the homologue of the dentate nucleus of human anatomy, the interpositus is homologous to the globosus and emboliformis. The three nuclei receive their afferents from different parts of the cerebellar cortex, the n. fastigii from the vermis, the interpositus from the medial and the lateralis from the lateral part of the hemisphere. The anterior lobe of the cat, incidentally, does not have a true lateral part. The flocculus projects to the vestibular nucleus. Then follows a detailed account of the efferent pathways, the various components of the brachium conjunctivum, the fasciculus uncinatus, etc., which is good and clear. The efferent connections in man are given as a separate chapter towards the end."

### 17.7.7.2.3 Other aspects of the cerebellar circuits of the interposed nuclei

Von Bonin also provided a guide to the remaining chapters of the book by Jansen & Brodal,

> "There follows a short (pp. 249-261) chapter 4 on the descending connections to the inferior olive by Walberg. On the whole it is very clear. But I have been unable to puzzle out figure 72. What does "dorsal" and "ventral" mean? Probably "cranial" and "caudal," but why were these words not used? It is of special interest to find that there is a strong projection from the aqueductal gray of the midbrain to the inferior olive. That there is also a cortical, a caudate, a pallidal and a projection from the nucleus ruber, is better known. That all the projections partly, but only partly, overlap may also be of interest, although little is made of it in the book.
>
> Then comes another short chapter 5 by Harkmark on the rhombic lip and its derivatives in relation to the theory of neurobiotaxis. It goes from page 264 to page 280, and it is a sane and modern account of a theory that should have long since been discarded. Piatt is cited at the end, "When theories of forty or more years standing have received so little experimental substantiation, it behooves us to invoke them less and experiment more. "
>
> The 6th chapter, by Jansen and Brodal, is perhaps the most interesting of all. It has as its heading, 'The structural organization of the cerebellum,' and *it stresses less what we know, and more what we do not yet know about the cerebellum*. It starts out with the flocculonodular lobe, which is mostly vestibular, but shows some interesting differences between flocculus and nodule. Extirpation of the former led to

extension of the hind limbs and flexion of the forelimbs, while the extirpation of the nodule led to the opposite symptoms. In discussing the possible role of the flocculonodular part on eye movements, it appears that the monkey and the guinea-pig behave differently, that there is, in other words, a species difference which it may be well to bear in mind in other cases as well.

Then follows the anterior lobe. Three divisions, the vermis, the intermediate and the lateral region should be distinguished. The vermis receives almost exclusively spinal afTerents via ventral spinocerebellar tract and the spino-olivary system as well as impulses via the dorsal spino-cerebellar tract, the external cuneate and the lateral reticular nucleus. The intermediate part does not receive impulses from the ventral spino-cerebellar tract or the inferior olive, but does receive pontine fibers relaying impulses from the cerebral cortex. The lateral part receives only cortical impulses via the pons. The somatotopical organization is somewhat difficult to understand, since it is missing in many of the afferents to the anterior lobe. The idea is advanced that the lateral reticular nucleus which shows a comparatively good somatotopical organization and seems to respond first of all to the spinal afferents, is the one responsible for giving the local sign. Also several pathways may transmit more than one kind of impulse. Thus the dorsal spino-cerebellar tract transmits not only proprioceptive, but also exteroceptive impulses. There is very little topological organization in the relays. Inhibition and facilitation from the cerebellum are so far more bewildering than clarifying. It may be wrong, according to the authors, to look for a somatotopical organization in the reticular substance, it may be that the topical arrangement is situated in the afferent system. It should finally be mentioned that the nucleus fastigii has different connection in its rostra1 and its caudal part. Vestibular fibers may end only in the caudal part of the nucleus.

For the purpose of this chapter the vermis of the posterior lobe is divided into two parts: the lobulus c2 on the one, and the pyramis and uvula on the other side. The former is the phylogenetically younger one. Lobulus c2 is mainly under the influence of the cerebral cortex via inferior olive and pons. It is that part of the cerebellum which receives audio-visual impulses. Uvula and pyramis are under the influence of the spinal cord and under that of the perihypoglossal nucleus and the medial reticular nucleus, thus indirectly also under that of the cerebral cortex. The pyramis is similar to the anterior lobe, but is more concerned with eye movements, while lobulus c2 is mainly concerned with the reception of acoustic and visual stimuli. This segregation of visual and oculomotor mechanisms is at the moment inexplicable.

Very little is said about the lobulus simplex.

In the ansiform lobule, the crus primum receives impulses from the caudate nucleus, pallidum, nucleus ruber and periaquaeductal gray, the posterior crus from the periaquaeductal gray and the cerebral cortex. What exactly that means, we do not know yet, but it should be borne in mind that the intercrural fissure may be of greater importance than commonly admitted. The middle folium seems to be related to the forelimb, the posterior folium to the hindlimb. While not everything fits in with this idea, the general implication that the ansiform lobule is related to the extremities is accepted.

The paramedian lobule is not too well understood, it receives some spinal afferents and also afferents from the olive and the pons. The olivary fibers appear to be non-spinal, while those from the pons may well be spinal. On the other hand, there may be cortical impulses relayed, as we know from experimental work, through the pons, from the somatomotor and the sensory area of the cortex. By and large the paramedian lobule appears to be concerned with the extremities, the anterior part with the forelimb, the posterior part with the hindlimb.

The paraflocculus may have to do with regulation of the axial musculature, or, in view of the rather plentiful supply with fibers from the periaquaeductal gray, with the regulation of autonomic functions.

The chapter concludes with some general remarks on the afferent and efferent cerebellar systems, on the cerebellar cortex and on cerebellar localization.

It appears to be clear that the flocculonodular lobe is concerned with the vestibular apparatus, the rest of the cerebellum is not so easily put into a certain category. That there are three longitudinal zones in the anterior lobe, seems clear, although it should again be emphasized that the cat has only the middle and the inner ones. The authors come back once more to the question of the somatotopic. organization, again without solving it. Finally they refute Edinger ’s terms neo- and palaeo-cerebellum, which are apt

to confuse rather than to clarify our conception of the cerebellum.

It is interesting that nowhere in this chapter issue is taken with the assumption that the cerebellum is part (and perhaps the most important part) of a servomechanism which would include the so-called extrapyramidal structures, several of which send their impulses to the inferior olive. That might have clarified quite a lot, for on that basis it might be quite unnecessary to look for a detailed somatotopic organization. The cerebellum might act on that part of the motor apparatus which happens to be most active. Whether such an idea could be entertained seriously, could easily be investigated experimentally.

There follows a 7th chapter by Torgersen on the Occiput, the posterior cranial fossa and the cerebellum. It ends with some phylogenetic considerations which are interesting, although they somehow do not quite fit in with the tenor of the rest of the book."

### 17.7.7.2.4 Schematic of cerebellum & interposed nuclei

Based on the interpretation by von Bonin of the material from Jansen & Brodal, **Figure 17.7.7-2** illustrates the position of the cerebellum in the overall neural system.

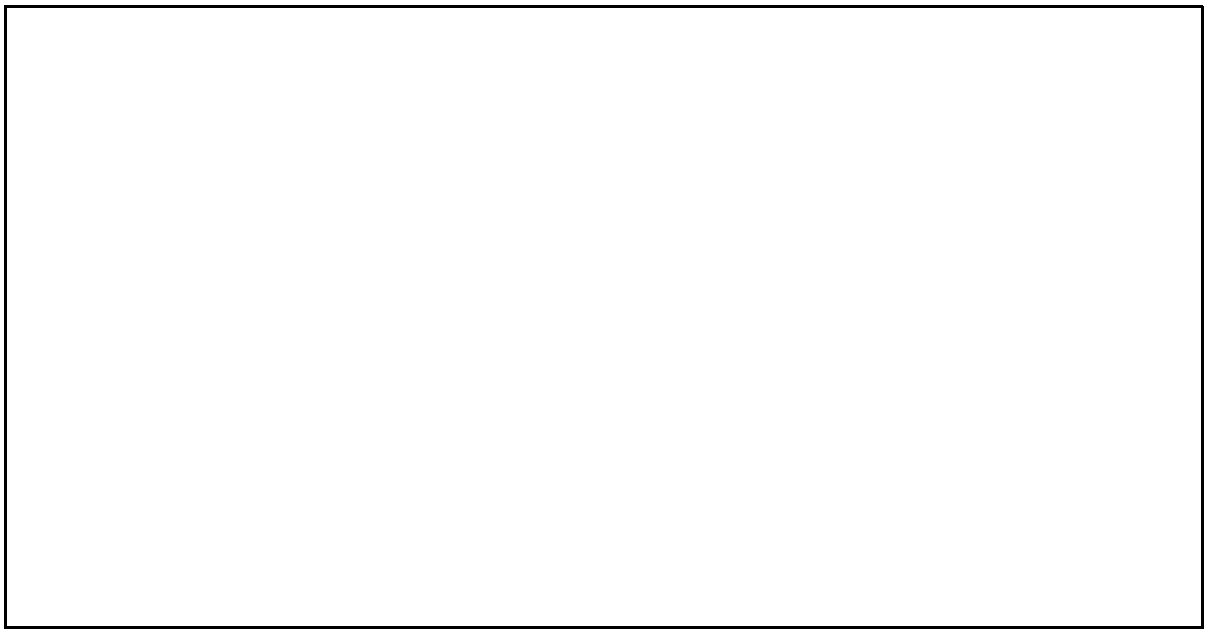

**Figure 17.7.7-2** Schematic of cerebellum in the context of full neural system ADD. Lateralis is homolog of human dentate nucleus. Interpositus is homolog of human globosus and emboliformis.

### 17.7.8 Proposed analog computer used within the CNS, Cerebellum, Basal Ganglia, etc.

[xxx empty

## 17.8 Challenges in using the Standard Model of Memory

The validation of the proposed Standard Model of Memory cannot be accomplished until the structure of the bytes used to store both the records and the indices used to store the information about the past history of the individual and his environment. This problem is similar to that overcome in the field of genetics. Overcoming the genetic problem took place in steps over a long period of time due to limitations in the technology available during that period. Major advances only occurred in abrupt changes due to both the available technology, and new thinking among the researchers. The same sequence of events took place in database design over a much shorter time period because of significant advances in both the technology available and the educational level of the researchers. The understanding of the neural memory storage system is currently at the stage of Mendeleyev in the 1860's.

The most profound impediment to moving forward in discovering the most fundamental of the fundamentals of neural computing and memory storage is ***to recognize the neural computing "machine" is an analog computer, and not a digital or even a binary computer.*** The bytes associated with an analog computer may be a function of the signal to noise ratio maintainable in the byte structures used. By their character, these bytes may be particularly suitable to employing fuzzy mathematical logic in the matching of patterns.

A dynamic range of about 200:1 appears to be used widely in the PBS when processing analog signals and

when determining the distance between Nodes of Ranvier. Thus, it is conceivable that the index byte might be based on a five bit amplitude code and a length compatible with a few pulses of a stage 3 signal propagation neuron. a Stage 3 signal propagation pulse rate of 200 to 500 pulses per second is commonly achieved in the auditory modality of humans.

> The limitation in the use of byte serial/bit serial encoding of the indices associated with memory processing is a major reason to assume byte serial/bit parallel formatting of the index bytes and the record bytes within the CNS. ***Byte serial/bit parallel formatting is the only known method to achieve sufficient speed of operation within the CNS*** to accommodate the behavioral responses measured by psychophysicists.

Byte serial/bit parallel encoding of indices offers a much wider index capability, the limit on the number of position bits can be as large as the number of neurons that can be included in a neural fascicule (bunch) between two engines. The ability to trace fascicules has recently been greatly expanded using diffusion tensor MRI, dtMRI (**Section 10.6.2.1**). dtMRI allows the course of a fascicule of myelinated neurons to be tracked by what has come to be called tractography. Unfortunately, the resolution of current dtMRI technology may not be fine enough to track individual fascicules. It is definitely not adequate for determining the number of neurons in a fascicule. The computer aided computations involved in collecting this type of data makes it also subject to artifacts.

The use fo byte serial/bit parallel encoding also offers the capability of using more complex encoding such as that used in modern man-made encoding, such as JPEG and particularly MPEG. These techniques lead to a very large degree of data compression, at the expense of some truncation of the data or some fuzziness in the index information.

The use of some higher level encoding, such as MPEG or JPEG, may aid in understanding the synaptic organization of climbing fibers at pyramidal cells of the cerebellum, and the form of the rosettes, or glomeruli, of mossy cells[111] within the cerebellum (and other elements).

The neural computing machine is fundamentally asynchronous. It does not employ a master clock. Instead, it frequently employs different lengths of cable (generally stage 3 signal propagation neurons to maintain time synchronization between related signals traversing significant distances (typically over 2 mm) within the CNS, and occasionally within the PNS.

> Variable length stage 3 signal propagation neurons are particularly prominent in the CNS (Meyer's loops) in order to accommodate the variable length neural paths associated with the curved paths of similar stage 3 signal propagation neurons following the curvature of the retina in the visual modality. Similar techniques appear to be used in the auditory modality to compensate for the method of audio spectral analysis employed (the Marcatili Effect, **Section 8.3.xxx** and **Section 4.4 in PBH**).

While emulations of an analog computing machine may by made using a digital computer, it is critical to keep prominently in the researchers mind he is dealing with an emulation and not a simulation of another binary computer.

## 17.8.1 Developing a protocol for discovery of the index bytes employed

The most important, and demanding, challenge to discovering how memories are manipulated is to discover the characteristics of the records stored and the characteristics of the indices used to store these memories. Few clues can be offered based on database science until some initial progress is made by brute force methods. Once a few likely characteristics are identified, database science will be able to narrow the search protocol significantly.

At this time, the neural database can be considered a relational database management systems, RDMS, based on a flat file and employing a separate indexing system. These are similar to the original assumptions, at the time largely conceptual, by binary computer scientists in the late 1930's.

---

[111]Scharfman, H., Sollas, A. Berger, R. & Goodman, J. (2003) Electrophysiological Evidence of Monosynaptic Excitatory Transmission between Granule Cells after Seizure-induced Mossy Fiber Sprouting *J Neurophysiol* vol90, pp 2536–2547.

An estimate of the size of the index word can be found in the expansion of the Windows, and other operating systems, from 32 bit bytes to 64 bit bytes around the year 2000 when the number of records to be stored exceeded the number of addresses available within a 32 bit byte, ~2 billion. The neural system of humans, and probably other primates, is known to require and to exceed this value. Currently, man-made systems with special requirements are using what is generally known as "double precision" mathematics. Double precision" implies the use of two (or more) bytes of the available index byte (word) to provide even greater address space.

*The character of the index byte in a basically analog form of neural computer is currently unknown and must be determined early in the discovery protocol.* It will probably be most expedient to find the mean number of neurons in a group of fascicules to determine the number of bit positions being transmitted in parallel within a given area of the CNS.

### 17.8.2 Developing a protocol for discovery of the record bytes employed EMPTY

The problem of discovering the bytes used to describe the information content of one record may be equally, or more, difficult than that associated with finding the bit width of the indices. [xxx expand ]

### 17.8.xxx The potential capability of a pair of climbing and pyramid cells EMPTY

The graphics of **Section 17.xxx** attributed to xxx can be interpreted in a variety of ways based on the Electrolytic Theory of the Neuron.

## 17.9 The Emerging Architecture of stages 4, 5 & 6 (2019)

As a result of the intense analyses associated with understanding of the pulvinar in Appendix ZH in "Processes in Biological Vision," it is now possible to expand the emerging architecture of the neural system from the proposal of 2018 in **Section 17.7**. The expansion is in the areas impacted by the pulvinar. The main conclusion is that the pulvinar and occiptal lobe work in parallel with the occiptal lobe focused on the awareness mode (where are things in the visual field) and the alarm mode while the pulvinar is focused on the analysis mode (what are things in the visual field).

It is arguable that the pulvinar is more important than the occipital lobe based on multiple facts;

- The clinical observations of humans with damaged or destroyed occipital lobes who can still perceive the external world well enough to read a newspaper,
- The academic investigations of Benevento & Port in 1995, showing that signals from the retina arrive at the pulvinar before they do at the occipital lobe,
- The evidence from the Benevento team that the inferior pulvinar is the source of the fine version and vergence signals for the precision optical servomechanism system, POSS, to establish important features in the visual field at the fixation point,
- The fact that the foveola/PGN/pulvinar pathway is responsible for recognizing and identifying objects in the visual field of the foveola (operating at maximum acuity,
- The strong liklihood that the pulvinar is the site of the stereopsis mechanism.

These facts are supported by the role of the ex-fovea/LGN/occipital pathway in

- providing the awareness mode for the total visual field, at low acuity,
- providing the alarm mode to alert the thalamic reticular nucleus, TRN, to engage the foveola/PGN/pulvinar pathway,
- providing the coarse version and vergence information to the POSS, to direct the eyes to a new point of fixation, while the foveola/PGN/pulvinar generates the fine pointing information internally.
- the ability of the visual modality to operate without the occipital lobe, especially in those individuals that lose this morphological structure at a young age (where plasticity plays a role),

## 17.9.1 Describing the proposed block diagrams of the visual modality–2019

**Section 15.6.9** of this work will describe the recent changes in the top level diagrams of the visual modality (2019). With regard to memory, they have not changed significantly since 2017, as developed in **Section 17.7**.

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