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Of Bits and Logic: Cortical Columns in Learning and Memory

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Despite the growing research and theoretical formulations tied to memory storage within the brain, the role of cortical columns has received relatively little attention. The current paper presents a theoretical formulation based on cortical columns as the binary units that contain all cortical information, and how memory and learning may occur based on the interaction patterns of columns. The described model is an extension of Lurian views, and suggests higher functions to result from the interaction of five systems. Specific mechanisms by which the thalamus and cortex interact to create long term memory formation are delineated. There is the suggestion of two distinct, but interactive, sensory—cortical memory systems, one for factual/generic memories and the other for episodic/personal memories. Hemispheric lateralization of function is explained on the basis of speed and quantity of columnar activation. Conclusions focus on recent technological advances that may allow cortical models to be testable in the near future.

Keywords: cortical columns, learning, memory

The cortical column has been proposed as the basic unit for the cortex (Calvin, 1995; Collonier, 1966). Mountcastle (1957) — who pointed out that neurons with similar response properties grouped into territories or columns across the thickness of the cortex — first described the existence of the cortical column. As noted by Cechetto and Topolovec (2002), columnar organization occurs in somatosensory, auditory, and visual primary receiving areas of the cortex, such that specific columns respond to discrete stimuli from the periphery. In the human motor cortex, there are also columnar aggregates. Forty percent of neurons in the aggregates project to a single motoneuron pool in the spinal cord; the remainder project to the motoneuron pools of muscle

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groups active in similar movements (Mountcastle, 1997). Over the years, this basic concept of columnar organization seems strangely absent in neuro-psychological theories of memory. In a recent text, *Neuropsychology of Memory* (Squire and Schacter, 2002), there is an absence of discussion of the cortical column. There are specific areas and structures in the brain discussed, though there is a failure to suggest how sensory and motor information is transduced, processed, and encoded, within these structures, most notably the cortex.

Mountcastle (1997) has provided an excellent review on the columnar organization of the neocortex. There are several points he makes that relate directly to any viable theory of memory based on the cortical column. He notes the columns show little variability in size across species and that cortical expansion in evolution is achieved by expanding cortical surface area with little change in cortical thickness. Rakic (1995) indicates this expansion is generated by an increase in the number of cortical columns. Therefore, it would seem likely that a theory of human memory and learning would need to explain how increasing the number, not size, of columns could lead to the development of higher cortical functions.

Another point made by Mountcastle is that a cortical column is a complex processing and distributing unit that links a number of inputs to a number of outputs: notably that efferent neurons in different layers project to targets (e.g., cortical to cortical versus cortical to sub-cortical); thus, indicating that intracolumnar processing operations leading to those different output channels may differ in some fundamental way. In reference to a theory of memory, there would necessarily have to be an explanation of column and cortical layer relationship.

Mountcastle indicates that dynamic physiological mechanisms, in part, maintain columnar organization. Afferent sub-cortical inflow sets the basic defining properties in some cortical areas, while intracortical processing does this in others. Therefore, a viable theory would need to explain such dynamic physiological mechanisms and how these interrelate with meaningful information.

Finally, he notes, "... brain operations and particularly those of the higher functions are distributed in nature, with some hierarchical and quasi-serial linking operations to the great afferent and efferent systems of the brain. The distributed mode of operation pertains particularly to the homotypical cortex and its reciprocal linkages to sub-cortical structures . . ." (p. 717). Thus, he provides an indication that any model of cortical functioning must involve both an explanation of the role of the column and how sub-cortical structures interplay.

If the cortical column is the basic unit of cortical functioning, it would be logical to assume that the only possible way cortical functioning and memory storage can be understood will require theories to address this level. The

current paper proposes that columns are the basic binary units (bits) arranged in specific ways (i.e., logic) to allow the coding and decoding of cognitive information. Logic refers to the manner in which bits interact (e.g., switches and gates). There should be a logical arrangement of the bits based on the nature of sensory input (e.g., auditory processing being related to sequential pressure analysis leading to a sequential pattern of processing in the temporal lobes), but allowing relative, adaptive memories (e.g., learning one's native language).

As the foregoing information would suggest, the current theory would be considered one of connectionism. Although the original connectionist model dates back to a 1943 paper by McCullough and Pitts, there have been periods during which the concept fell in and out of favor. In his thoughtful review on the history of connectionism, Pollack (1989) reaches the following conclusion:

Like many systems considered historically, connectionism seems to have a cyclical nature. It may well be that the current interest dies quite suddenly due to the appearance of another critical tour-de-force such as *Perceptrons*, or, a major accident, say, in a nuclear plant controlled by neural networks. On the other hand, some feel AI is entering a retrenchment phase, after the business losses recently suffered by its high-profile corporate entities and the changing of the guard at DARPA. Given that it doesn't all go bust, I predict that the current limitations of connectionism will be understood and/or overcome shortly, and that, within 10 years, "connectionist fractal semantics" will be a booming field. (p.17)

Although his prediction of a booming field related to connectionism in ten years was not accurate, Pollack certainly believed that connectionism was far from dead. Instead, he held the opinion that the field had not evolved far enough to provide a sound explanation of how connectionism is accurate. In actuality, binary (i.e., a neuron fires or does not fire) synaptic connections are present throughout the nervous system and the information reflected in nerve propagation is fixed (i.e., law of specific nerve energies). It would seem inconsistent, both ontogenetically and phylogenetically, for this pattern not to exist at the cortical level. Within the field of clinical neuropsychology, disconnections of cortical areas are accepted explanations of the various agnosias and other cognitive problems (e.g., conduction aphasia).

The current theory proposes a model to explain how the cortical column can act as the basic unit of information, taking into consideration its interplay with sub-cortical areas. Unlike prior connectionist models, it provides: implication for the role of sub-cortical and cortical structures; specific suggestions on the transduction methods employed in the cortex; and feed forward and feed backward mechanisms both proximally (i.e., nearby cortico–cortical projections) and distally (e.g., cortical to sub-cortical to cortical projections, frontal cortical to posterior cortical). Prior to an elaboration of the model, a brief discussion of columns is warranted.

Minicolumns and Macrocolumns

Two levels of vertical organization of columns have been identified — minicolumns and macrocolumns (Calvin, 1995). Minicolumns contain between 100 and 200 neurons with a diameter of about 30 μ m, whereas macrocolumns seem to contain at most several hundred minicolumns that have a diameter of 0.4 – 1.0 mm. If a cortical bit of information exists, it could feasibly be a single neuron, a minicolumn, or a macrocolumn. In considering the level at which bits exist, there are at least two important factors based on the current model. First, a bit must be resistant to damage since the integrity of each bit is critical for the functioning and information representation of interconnecting bits. Second, it has to allow for the existence of very large volumes of information bits in a small area.

If single neurons were bits, that would meet the large volume requirement, but these would not be resistant to damage. In this case, destroying any single neuron would have devastating effects on interconnecting bits. Minicolumns would be more resistant to damage since 100 or more neurons are present. However, it is doubtful that the several million minicolumns estimated to exist within each of the 52 Broadmann areas (Calvin, 1995) could adequately explain the large information capacity of each human cerebral hemisphere. The macrocolumn would obviously be the most resistant to damage. At face value, the macrocolumn would appear to be the least capable of meeting the large information storage requirement. However, there is a manner in which this could occur. The macrocolumns could be overlapping; thus, there would be an exponential increase in the number of bits by sharing minicolumns. Additionally, the fact that the boundaries of macrocolumns are constructed of minicolumns, the expected strong inhibitory field around the macrocolumn would prevent the activation of other macrocolumns that share minicolumns and would be structurally resistant to loss of integrity with the death of single neurons in the minicolumns. Finally, at the more complex levels of processing (e.g., multisensory, relational), it is possible that the macrocolumns are most typically temporary in nature such that those minicolumns do not become "dedicated" to any single macrocolumn.

If such an overlapping arrangement occurs, a number of macrocolumns can share a common minicolumn, though there are a large number of unshared minicolumns for each. The inhibition around column boundaries can prevent the activation of the wrong macrocolumn that shares one or more minicolumns. If two macrocolumns are bits related to a particular stimulus parameter (e.g., color), there would be no sharing of minicolumns between those two macrocolumns and their adjoining macrocolumns. This is due to the possibility of simultaneous activation of both with a stimulus input. That could explain the observation of macrocolumn distances between color sensitive

"blobs" which are interspersed with surrounding regions more sensitive to visual form in the primary visual cortex (Bartfeld and Grinvald, 1992). Similarly, it would be consistent with the observation that somatosensory strip neurons responsive to skin stimulation alternate with those specializing in joint and muscle receptors at distances of about 0.5 mm (Mountcastle, 1997). The finding that a number of minicolumns within a given ocular dominance macrocolumn are responsive to different orientations of lines and angles (Hubel and Wiesel, 1977) could be explained as these minicolumns being activated as part of overlapping macrocolumns. In reality, each bit could be at the macrocolumn level.

Calvin (1995) notes the unusual pattern of superficial pyramidal neurons that suggest a macrocolumnar organizing principle. The collateral axon travels a characteristic lateral distance without giving off any terminal branches; then it produces a tight terminal cluster. The distance to the center of the terminal branch is about 0.43 mm in primary visual cortex, 0.65 in the secondary visual areas, 0.73 mm in the sensory strip, and 0.85 mm in the motor cortex of monkeys. It may then continue for an identical distance and produce another cluster, in some cases continuing for several millimeters. This suggests the size of each macrocolumn is determined by the cluster distances. Within the current model, this explains how macrocolumnar organization can develop based on environmental interactions.

The millions of minicolumns and their interconnections would be "hardwired" at birth. The macrocolumns of the primary receiving areas would be the first to form based on sensory relay thalamo—cortical connections. As an example, let the primary receiving macrocolumn consist of 100 minicolumns. The 100 minicolumns' cortico—cortical axons would project in multiple directions. The intersection points where the axonal terminal bundles of two or more primary receiving macrocolumns' efferent projections meet would become the new bit (i.e., new macrocolumn) composed of a similar number of minicolumns. The new macrocolumn then passes along its efferent activity in a similar manner, intersecting with the efferent activity of other macrocolumns. Each intersecting "bundle" of minicolumns becomes a new macrocolumn. Over time, further enhancement of the functional integrity of a permanent macrocolumn may occur by the death of unused pyramidal cells in minicolumns projecting axons in unused directions.

Language development illustrates this concept. The primary receiving area macrocolumns can represent frequency and intensity of auditory information. The primary receiving area macrocolumns activated would be those corresponding to the characteristics of the language spoken around the infant. Relative frequency (voice variations) second-order macrocolumns would be the first to form. Logically, there would be a number of relative frequency macrocolumns for a particular phoneme (due to different voices), which in

turn, provide efferent activity to form additional macrocolumns. Eventually, there would be one macrocolumn, which represents all the lower-order relative frequency columns for a given phoneme. This column would be the bit for that specific phoneme. The sequential pattern required for phoneme macrocolumns to activate the new location of word macrocolumns is determined spatially. Since the axonal projections of all phoneme macrocolumns that comprise a word are activated in a specific order, the first activated will have its efferent activity travel further than the next one activated. The spatial location of the new word column will be determined by the efferent travel distance associated with the location where the two or more phoneme macrocolumns' axonal terminal branches meet. This new word column would now reflect inflection (i.e., louder versus softer; abrupt versus elongated sound) and placement (i.e., sequential order) of phonemes for the newly learned word. The lack of hardwiring of macrocolumns at birth would allow for the plasticity needed to learn the particular language(s) used in a child's environment.

Lateralization of function would likely be the result of both predisposition and environmental stimulation. If both hemispheres are fully intact, it would be expected that each would follow its predisposition as the macrocolumns are formed. One possible predisposition might be how the terminal branches of the minicolumns' superficial pyramidal cells develop their neural connections. The axonal boutons associated with each branch can synapse to create either excitatory or inhibitory effects. The more inhibitory terminal branches that exist along the axon, the fewer the number of macrocolumns expected; the more excitatory terminal branches that exist, the larger the number of macrocolumns expected. Alternately, there might be fewer terminal branches at greater distances in one hemisphere versus the other at birth. A third influence could result from interhemispheric fibers that inhibit macrocolumnar formation in the opposing hemisphere; thus, macrocolumns in one hemisphere using one mode of operation could in turn decrease the opposing side's use of that same mode. Regardless, if fewer macrocolumns at greater distances are present, quicker but less detailed processing can occur. The greater the number of macrocolumns in closer proximity, the slower but more detailed the processing. One final point is that each hemisphere's sensory processing mode would necessarily lead to a similar processing mode of its frontal lobe. This is based on the expectation that the frontal lobes' macrocolumns will develop in association with afferent activity from the posterior regions. Once the mode of operation is determined, higher-order frontal macrocolumns continue this pattern.

From this point forward, the term "column" refers to a macrocolumn and is the proposed basic binary unit for cortical information. In reference to the overall organization of information of columnar bits, the organizational arrangement is one in which sensory input must be coded as processing moves distally from the primary receiving areas toward association regions. As will be noted in subsequent sections, this is viewed as moving from less-organized, or lower-order, information bits toward more-organized, or higher-order, information bits. The previous example of word columns reflects the proposal that two (or more) less-organized bits (e.g., phonemes) can reflect two or more parameters of the same raw stimulus input. When activated by the input, each bit can project axonal inputs to a common column. This common column could be activated only when both inputs occur. This common column is more-organized since it reflects the information from two or more columns associated with relatively raw stimuli.

A Dimensional Systems Model

Any theory attempting to explain the myriad of data on higher cortical functioning cannot be attributed to a sole author. Instead, it represents the assimilation of previously suggested mechanisms by numerous authors, as well as the incorporation of numerous research findings and interpretations. An example of this is Luria's (1966) theory regarding higher cortical functions. Despite his unique contributions to the neuropsychological literature, his theories were dependent on the work of other notable scientists (e.g., Hughlings Jackson). The current model similarly is the result of an assimilation of other's works, including that of Luria.

To allow the reader to gain an understanding of the model, an overview is first presented. Next, there is a more detailed analysis of the systems. Finally, there is a discussion of aspects as related to the independent development of memories in each hemisphere.

Overview of the Model

There are five basic systems proposed to explain higher cortical functions. Within the model, subcortical functions are integral in our understanding of these higher functions. It is important to note that in the discussion of these subcortical functions, there has been a necessary simplification to reflect how these can interact with the cortical system. Therefore, the reader should not regard the described functions as the sole activities of the various subcortical structures.

The five basic systems are the sensory input system, the arousal system, the attention—memory system, the cortical system, and the motor system. The arousal system is subdivided into the general arousal system, the limbic system and the biological needs system.

The sensory input system is involved with providing the cortical system with necessary environmental information. Obviously, without information from the environment, including ongoing feedback as to the organism's ongoing behavioral responses, little meaningful activity can occur. The three most

important sensations for higher functions appear to be vision, audition, and touch/kinesthesis. Although smell and taste do greatly influence certain forms of behavior, their influence on higher functions appears limited.

For the brain to react to sensory information, it must have power supplied. Providing the power for all brain functions is the responsibility of the general arousal system. The general arousal system has an optimal functioning range, which, if maintained, allows the most efficient operation of the cortical system.

Two additional "power supplies" are the biological needs system and the limbic system. With deprivation of a biological need (e.g., hunger, thirst), an increase in cortical arousal would be expected. Such a heightened arousal would have survival significance in that no change in general behavioral arousal would result in a lowered possibility of meeting the need. As the need increases, it would seem logical that subcortical and cortical learning/memory functions would function at optimal levels.

The limbic system refers to those structures involved with both positive and negative emotions. This system would increase general behavioral arousal whenever there is a change or increase of emotion tied to short term external factors responsible for the change. It would be of biological significance to have heightened cortical arousal and, thereby, increased memory functions in response to environmental situations that cause emotional arousal. In the case of positive emotional arousal, often the result of meeting a biological need, there would be enhanced memory for the situational context. In a similar fashion, increased arousal and enhanced memory during negative emotional states could result in the learning of situational cues and effective responses for future situations that are similar. In contrast, there would be decreased behavioral and emotional arousal for long term, unchanging factors that are continually present since there would be no survival value to maintaining that arousal.

Although arousal from these three systems is necessary for the formation of long term memories, the arousal would still require channeling through a memory control system before reaching the neocortex. The system responsible for such control would require: (a) input from the arousal (i.e., power) sources; (b) input from the sensory receptors; (c) connections with the cortical columns (i.e., information units) for the development of new or enhanced interconnections (i.e., memory formation); and (d) the ability to coordinate the activities of these inputs and outputs via reciprocal connections (i.e., attention). This proposed system is the attention—memory system.

Provided adequate arousal is present, the attention—memory system activates whenever sensory input occurs to the cortex. The next step would involve the reception, by the cortical regions responsible for directing attention (i.e., frontal attention centers), of a signal that potentially important sensory information is being registered at the cortical level. Once activated, the

attention centers would then perform several functions. First, they would provide enhanced focus on the source of the sensory information if the stimulus required further analysis. Next, via their direct connections with the cortical regions that originally processed the sensory input, the attention centers could re-energize or re-excite those same cortical regions (i.e., short term memory). Finally, the attention centers could activate a closed circuit or loop involving the arousal systems input and the cortical columns in the regions activated by the sensory input and motor response (i.e., long term memory formation).

The concept of multiple frontal attention centers goes beyond columns lateralized in each hemisphere. Lateralized frontal activation does occur in relation to the nature of the stimulus processing and response (e.g., Wagner, 2002), but the current theory suggests any number of different frontal columnar arrays can control different attention and response patterns in the same hemisphere. Anytime a verbal response is required in any experimental memory task, left frontal activation in and around Broca's area would be expected. However, such activation does not necessarily imply this area is controlling all attention processes. Wagner (2002) notes examples tied to working memory in which left dorsolateral frontal activation is seen in certain tasks, in addition to ventrolateral activation. This has been interpreted as the left ventrolateral frontal cortex accessing posterior sensory information while the dorsolateral cortex manipulates the ventrolateral information. Within the current proposal, the columns in each of these frontal areas would be involved in coding and decoding the manipulated information, and would activate the proposed subcortical long term memory process. If a different task analysis occurs, the columns in a different frontal region would be the attention center involved in the activation of the long term memory components.

Once the sensory input reaches the cortical primary sensory receiving area, subsequent organization of the input must allow the organism to react in a meaningful way. Such processing is done by the cortical system, which may use up to four dimensions in the analysis of a single input. These four dimensions are: (a) unorganized—organized; (b) simultaneous—sequential; (c) sensory—nonsensory; and (d) analytical—global.

As previously mentioned, the dimension of unorganized—organized will always be present in the processing of sensory information at the cortical level. As an example, let us consider how representation (i.e., memory) of an individual letter of the alphabet may be stored. As information reaches the primary receiving area of the cortex, it arrives in a point-to-point manner. Therefore, individual columns that represent binary information activate. The primary sensory information columns can then activate columns reflecting specific line orientations, which in turn all send connections (i.e., the information stream) to a common column (the letter column) that activates. This letter column can, via its connections to even more-organized columns, result in

meaningful behavior. This simple sounding process would likely take a large number of primary sensory columns, with relatively fewer columns involved as the information stream progresses. This is the theorized additive process by which raw sensory information becomes meaningful symbolic stimuli.

The second dimension is that of simultaneous and sequential processing. Reynolds and Finch (2003) note the enduring of the simultaneous—sequential dichotomy into current theoretical and clinical practices. Within the current model, simultaneous processing simply means that a number of columns activate at the same time. In this manner, more-organized, or higher-order, information depends upon less-organized columns simultaneously activating. The previous example tied to visual information processing of a letter reflects simultaneous processing in which multiple lower-order columns project to a single higher-order column.

Sequential processing reflects one or a very few columns being activated at a given time. For a higher-order column to activate, the inputs from its lower-order columns must be received in a specific temporal pattern. Thus, if the order of stimulus input is altered, even though the same stimulus input occurs, a different higher-order column will be activated. In the primary auditory receiving area, the frequency and other sound qualities result in the activation of specific columns. The sequence with which these columns activate will then determine which higher-order columns activate. Thus, basic sounds in turn activate columns representing phonemes, which in turn activate "word" columns. Again, this is an oversimplification of a complex process but clearly communicates the method by which sequential processing would occur.

The third dimension is that of sensory—nonsensory. This distinction is particularly useful in understanding the perceived qualitative differences in visual, auditory, somatosensory, and nonsensory memories. On the sensory end of the dimension, memories can be unisensory or multisensory. In terms of memory storage (i.e., the set of columns containing the information), a unisensory memory would be expected to use only columns closer in proximity to its primary receiving area. Sensory memories have the quality of the sensory mode through which the salient information reaches the cortex. For the memory to be recalled with its original sensory qualities (e.g., visualizing in one's mind), the cortical stream, or circuits of columns, would be in direct connection with the columns near the primary receiving area for that sense. This appears consistent with recent imaging studies (Nyberg, 2002).

There appear to be two distinct types of memories. In reference to verbal memories, Lezak, Howieson, and Loring (2004) note a general recognition of two distinct, though interrelated, stores: episodic/event and semantic. Episodic memories are those of one's own experiences, being localizable in time and space. Semantic is what is learned as knowledge, being "timeless and spaceless," such as the alphabet or historical data. Given the similarity of the organ-

ization (i.e., primary, secondary, and tertiary areas) in each hemisphere as noted by Luria (1966), it seems only logical that both hemispheres would have both episodic/personal and factual/generic memories. Factual/generic memories likely involve information contained in the simultaneous/sequential columns of the parietal, posterior temporal, and occipital lobes. Episodic/personal memories would be related to the sequentially (i.e., time) processed columnar information in the anterior and medial temporal lobes. These systems would obviously have intricate reciprocal connections. The connections of the hippocampal and other medial temporal columns to the limbic structures and the frontal lobe columns would lead to the "familiarity" aspect of memories. The familiarity would involve an emotional component (i.e., limbic system) and time information (i.e., sequential processing of information). Recent research suggests that the medial temporal lobe is involved in the recollection of both recent and remote autobiographical memories (Steinvorth, Levine, and Corkin, 2005).

There is support for two different directions of travel of neuronal information tied to intelligible speech (Narain et al., 2003). Based on functional magnetic resonance imagery (fMRI) data, Narain et al. (2003) found both the anterior and posterior temporal regions activate. The current model suggests the anterior activation is associated with the personal/episodic informational aspect, while the posterior activation is associated with the factual/generic aspect.

Nonsensory memories refer to those not rooted in any particular sensory mode. These would be located in the frontal lobes. In the motor production of speech, for example, planning, programming, and execution involve the nonsensory cortical columns. In cases where no auditory sensory input occurs from the posterior cortical areas responsible for spoken language processing (e.g., conduction and Wernicke's aphasia), production of fluent speech can still occur, though its content is unrelated to the spoken language of others.

The fourth dimension of the cortical system is global—analytical. The distinction between these types of processing occurs at two levels — the area containing the information units (i.e., cortical columns) and the total number of available units processed. In contrasting the two processing types, global processing would have less total columns and/or columnar interconnections than would analytical areas when the surface area is equal in size. This does not necessarily imply there are fewer neurons in the same sized areas, just that there are fewer columns in an array associated with any given sensory input, analysis, planning and response.

The diffuse arrangement of information units in global processing would allow faster processing of novel stimulus input, but would sacrifice detailed analysis as a result. By processing faster, the information unit excitation/activation pattern (i.e., the information stream) could quickly gain access to cortical dimensions other than that involved strictly in the sensory region

where the input occurred. For example, if novel visual information (i.e., unisensory, sequential/simultaneous, unorganized) is received through global processing, its overall pattern (i.e., its gestalt) is quickly accessed and used in processing. If a quick response is necessary, the global nonsensory areas can provide a plan (i.e., simultaneous/sequential processing), a program (i.e., from more- to less-organized processing), and an execution via the motor system. However, the response will lack the carefully planned and exact nature that is possible through analytical processing.

When contrasting the functional utility of each processing type, analytical processing would be involved with stimuli and responses that require detailed analysis, a large volume of memory storage, and/or well learned materials (i.e., those encountered on a frequent basis that are behaviorally efficacious). Global processing would involve stimuli that are novel, require the maintenance of the overall pattern with few details, and/or require a low volume of memory storage. Examples of functions tied to global processing would be novel visual–spatial tasks, navigation in personal space, emotional analysis, and melody perception and reproduction. Analytical functions would include spoken language, reading, spelling and writing.

Since analytical and global processing appear to serve distinct purposes, then it seems reasonable that both would independently receive the same basic sensory input. Whichever type of processing is the most efficient and effective can provide control over the ensuing response. Such parallel processing would activate both hemispheres simultaneously, but allow semi-independent analysis of information. Since these are parallel in nature, then each hemisphere contains all cortical system dimensions.

The final system for higher cortical functions is the motor system. This system provides control over the voluntary muscles throughout the body. It has its origin in the cortical system in which the columnar information units go from more to less organized. At the least organized level, there is direct correspondence from each cortical column to a specific motor unit.

The foregoing overview of the dimensional systems model has provided a description of each major system and its components. The model explains higher cortical functions as interactions of peripheral and central nervous system components from the level of sensory receptor excitation to neuromuscular control of the response. With this working knowledge in mind, we will now turn toward a more detailed description of the model.

Neuroanatomy and Neurophysiology of the Model

The sensory input system refers to the peripheral receptors and the nuclei and tracts associated with sensory information to the thalamus and cortex. The general arousal system involves much of the reticular system. Its integrity is required for any higher level system to operate, including the selective arousal systems. The biological needs system anatomically relates to the hypothalamus, epithalamus, and brain stem structures involved in the maintenance of biological needs (e.g., the raphe nuclei). The limbic system consists of those structures historically termed as such, with recognition that there are difficulties in specifying the exact structures and their relational patterns (Price, 2002).

The attention—memory system includes the thalamus, the frontal lobes, and the interconnections of these areas to each other, other cortical regions, and the brain stem. Other authors (e.g., Crowne, 1983; Wagner, 2002) have suggested the roles of prefrontal and lateral frontal cortex in attention. In addition, Jones (1998) suggested the involvement of the dorsomedial nucleus and other association nuclei of the thalamus in memory.

The cortical system, as indicated by its name, is the neocortex. As will be discussed in detail, the activity patterns of and sensory input to the cortical layers and columns will determine the nature of any given higher function. The functions of this system are processing and integrating the incoming information from the thalamus and then developing plans of action based on that input.

The final system, that responsible for the overt expression of the organism's planned and coded responses, is the motor system. Its anatomical substrates include the basal ganglia, the cerebellum, portions of the thalamus, the motor and pre-motor areas of the cortex, and the fibers interconnecting the regions. With the basic systems identified, the discussion will now focus on the dimensions of each as they relate to higher cortical functions.

Sensory Input System

The three senses that appear to have phylogenetically determined the nature of higher cortical functions are vision, audition and touch/kinesthesis. The manner in which these sensations are processed at the cortical level can serve as a foundation for understanding all cortical functions. As will be discussed later, these senses vary along the simultaneous–sequential dimension. Specifically, auditory and somatosensory input is pressure related, requiring distinct forms of analysis. Auditory input typically requires sequential analysis while somatosensory input requires simultaneous analysis of various body regions. Vision involves both simultaneous and sequential analysis of information. Thus, the nature of the sensory input appears to have guided the types of processing seen in various cortical regions.

Arousal Systems

General arousal system. As indicated by Luria (1966), decreases and some increases in the activity of the brain stem reticular activating system will have

a direct influence on higher cortical functions, including attention and memory. The current model considers arousal in this region to be a necessary component for attention and memory activities to occur. The dimension along which activities of the general arousal system varies is termed aroused—unaroused. The extremes of this dimension are uncontrollable activity (e.g., manic state) and coma.

Biological needs system. This system includes all biological requirements for the survival of the organism and its species (e.g., eating, drinking, and sexual behavior). This system will vary along a deprived–satiated dimension at any given time and can influence selectively the input or arousal received at the level of the attention–memory system.

Limbic system. This system serves the role of determining the emotional state of the system, including initiating the physiological characteristics of emotions. Although there are a number of different emotional states (cf., Ortony, Clore, and Collins, 1988), all emotional states vary along a positive-negative dimension. Therefore, as the emotional state moves away from neutral in either a positive or a negative direction, selective arousal will occur and enhance the attention–memory system.

Attention-Memory System

A number of neurophysiological theories have been proposed to explain certain aspects of human memory (e.g., Horel, 1978; Mishkin, 1978; Scoville and Milner, 1957; Squire, 1982). Many theories have attended to *declarative* (i.e., verbally explicit) memory and tend to perpetuate the view that visual, motor, and emotional memory and learning represent different qualitative processes. The current model takes a different perspective in that it views cortical aspects of visual, verbal, motor, and emotional memories as resulting from the same basic rules of columnar interactions. It proposes that the thalamus is a crucial common denominator in the dynamic formation of any type of memory and that similar neurochemical and neurostructural changes of cortical columns explain all memory types.

The neuroanatomical structure of the attention—memory system would require: (a) input from the arousal system; (b) input from the sensory receptors; and (c) connections to the cortical columns. The only readily identifiable structure that meets these requirements is the thalamus. The fourth requirement of the attention—memory system is that it coordinates the activities of the inputs and outputs. This can result via the frontal attention centers and/or the anterior and medial temporal cortex to the dorsomedial nucleus.

The thalamic nuclei vary along an activated–inhibited dimension. The degree of general non-selective arousal depends on input from the arousal system. The proposed routes of thalamic input that control dynamic memory

formation are from the general arousal and limbic systems. The former connections are the thalamic reticular nuclei and the reticular input to the intralaminar nuclei of the thalamus, whereas, the latter connections refer to limbic input to the anterior and medial nuclear groups (Carpenter, 1976).

The thalamic reticular nuclei may be particularly responsible for general thalamic activation. These nuclei project fibers into the thalamus (Scheibel and Scheibel, 1966), and, as such, can provide an overall increase or decrease in thalamic activation. Other reticular input, as well as input from the thalamic reticular nuclei, can also influence the intralaminar nuclei. The intralaminar nuclei are involved with cortical activity, as well as influencing the thalamic "association" nuclei (i.e., dorsomedial, lateral dorsal, lateral posterior, and pulvinar [Starzl and Whitlock, 1952]). It is the intralaminar nuclei, cortical columns and "association" nuclei connections that are considered instrumental in long term memory formation. Other researchers (e.g., Jones, 1998; Paller, 2002) have also suggested the involvement of thalamic nuclei in memory.

The pulvinar nuclei are phylogenetically the most recent to develop in the thalamus. Human embryonic development shows that the pulvinar are the only thalamic nuclei to be telencephalic in origin (Ohye, 2002). The pulvinar nuclei interconnect with the posterior cortical areas proposed to contain the factual/generic memories. In contrast, the anterior temporal region interconnects with the dorsomedial nucleus and this is the system associated with episodic/personal memories. This is felt to be of importance in relation to memory consolidation of each type (i.e., episodic versus generic) since it is the thalamic association nuclei the current theory implicates in long term memory formation.

The direct thalamic input received from the limbic system reflects this system's influential role in attention and memory. However, this is considered but one part of a thalamo-cortico-limbic-thalamo feedback loop that will actually determine whether memories with affective qualities (e.g., conditioned emotional responses) will occur.

Any stimulation requiring attention is channeled through the thalamus and then is relayed to the cortex where it will be integrated and evaluated. Once the sensory information has entered the cortex, the frontal attention centers receive input from the posterior cortical regions associated with sensory reception (cf., the frontal eye fields in the theory of Crowne, 1983). The attention centers can then track and/or control subsequent cortical activity either directly, indirectly (i.e., via efferent input to the dorsomedial nucleus), or both. The attention centers to dorsomedial nucleus activation can feasibly lead to one or more feedback loops. One loop would be through direct reciprocal prefrontal connections between the two areas. A second would be the dorsomedial nucleus reciprocal connections to the anterior temporal lobe. A third would be dorsomedial nucleus connections to the intralaminar nuclei and

then via connections to the cortex. A fourth possible loop follows the intralaminar nuclei's activation or disinhibition of the "association" cortical regions. Once initiated, the intralaminar nuclei to association cortex, and intralaminar nuclei to thalamic association nuclei, circuits may be maintained for a time period after attention (i.e., attention centers to dosomedial nucleus involvement) has been shifted. Excitation of loops can occur via the previously described general arousal system efferent input to the intralaminar nuclei. In relation to declarative memory functioning, Van Der Werf, Jolles, Witter, and Uylings (2003) similarly suggest the role of the dorsomedial nucleus and anterior nuclei in the selection of material to be stored, as well as the coordination of strategies used to retrieve materials. They also suggest the intralaminar and midline nuclei maintain a necessary state of activity in the cortical regions involved in the memory processes. They believe the two types of function subserved by these thalamic nuclei, focusing on content versus state, need to work in parallel to mediate and allow memory functioning, respectively.

These processes can provide a neurophysiological explanation of immediate, short term, and long term memory. Immediate (e.g., iconic) memory is represented in the initial thalamic to cortical primary sensory receiving activity and subsequent activation of the frontal attention centers. Short term memory is represented by the feedback loops between the attention centers and other cortical areas. Short term memory would be aided by self-re-exciting loops occurring within the cortical columns (Eccles, 1977) such that these columns briefly maintain activity and, thus, could be located by the attention centers and reactivated. Long term memory occurs as a result of the intralaminar to association cortex and/or the intralaminar to thalamic association nuclei feedback loops. Once these latter feedback loops become operational, several processes would then occur at the cortical columnar level. Initially, subcellular processes (i.e., presynaptic, intrasynaptic and postsynaptic) can occur in existing intercellular connections between cortical columns (Woody, 1982). Such changes would influence the future probability of columnar activation. Over time, actual neuronal growth occurs (Thompson, Berger, and Madden, 1983; Woody, 1982). Obviously, by increasing neuronal connections to cells in a given cortical column, the afferent input to that column increases, as does that column's probability of activation from the afferent input.

The possibility of two independent processes (i.e., subcellular factors and neuronal growth) that are time linked leads to an interesting postulate of two distinct forms of long term memory. The initial phase would consist of subcellular factors. For the first few hours, such factors as presynaptic ionic concentrations would account for the increased probability of columnar activation. Afterwards, other more permanent influences, such as increased neurotransmitter/neuropeptide synthesis, storage and release, would increase the probability of cortical columnar activation under the conditions of a similar stimulus input.

The second phase of long term memory is reflected in gradual neuronal growth patterns (i.e., axonal sprouting and increased dendritic spines). Once a number of new neuronal connections had occurred, the memory is truly permanent, barring structural damages to the column or the sources its afferent input (i.e., lessorganized columns).

These processes could explain observations tied to priming effects and observed cortical activity patterns based on neuroimaging techniques. For example, it has been observed that increased posterior and frontal activity is seen during learning, with decreased activity patterns after learning (Hempel et al., 2003; Martin and Turennout, 2002; Wagner, 2002). The current theory suggests the increased frontal activity would be due to attention centers' involvement and short term memory activation of the posterior cortex where the sensory columns involved in the analysis are located. Additionally, the pulvinar to posterior cortex connections would occur to stimulate neurotransmitter increases in the involved columnar array. Once the neurotransmitter stores have increased, such that the less-organized columns easily activate the more-organized columns tied to the stimulus of interest, there is no need for increased frontal attention centers or pulvinar activity to initiate memory consolidation since this has already occurred (i.e., there is a memory represented by the associated columnar array). Kraut, Calhoun, Pitcock, Cusick, and Hart (2003) have shown that in recall of objects from visually presented features, there are noticeable differences in times of onset, peak, and return to baseline in the thalamus and cortex. Brodmann area 6 (BA6) was the fastest, with dorsomedial nucleus and pulvinar activity also being noted. The pulvinar demonstrated the slowest transients of all areas. These authors suggested that BA6 mediated the early designation or refinement of search criteria (an attention center as defined in the current paper), while the pulvinar might be involved in the binding of feature stimuli for an integrated object memory. Thus, the pulyinar could likely be involved in both memory consolidation and continued association.

Additional support for the involvement of the thalamus in memory consolidation comes from a recent case study of a forty-year-old alcoholic patient with Wernicke–Kosakoff syndrome (Fellgiebel, Scheurich, Siessmeier, Schmidt, and Bartenstein, 2003). He demonstrated improvement in his clinical state and neuropsychological performance that paralleled cerebral glucose metabolism improvements in the left anterior cingulate and parietal areas. However, he continued to show severely disturbed thalamic glucose metabolism and a severe amnestic syndrome.

The influence of the thalamo-cortico-limbic-thalamo feedback loop would be to enhance activation of the thalamic circuitry described above by increasing thalamic arousal directly. Indirect thalamic arousal would also occur via limbic system efferent connections (e.g., from the amygdala) to the perifornical

region of the lateral hypothalamus. This hypothalamic region has both neurophysiological and neuroanatomical data to support its control of the spinal intermediolateral cells, which, in turn, control sympathetic activation (Smith and DeVito, 1984). Increased sympathetic arousal could then create increased general arousal system input to the thalamus. If this aspect is correct, and if the cortical mechanisms described below are considered, then it is possible to explain certain aspects observed in learned emotional responses.

For example, Smith, Astley, DeVito, Stein, and Walsh (1980) observed that bilateral lesions of the perifornical region of the hypothalamus in the baboon eliminated the entire learned cardiovascular response complex completely and permanently. However, there was no effect on the behavioral indices of the conditioned emotional response. Within the current model, such a lesion would disrupt indirect thalamic arousal, though the direct limbic system connections to the thalamus would remain intact. This would leave the observed behavioral components intact. In another non-human example, McGaugh's (1983) work on amygdala stimulation and peripheral adrenergic enhancement of learning in rats is explained as the result of increased thalamic arousal input. More recently, there has been support of the role of enhanced human memory consolidation associated with increased arousal at encoding (Cahill, Gorski, and Le, 2003). Moss (2001, in press) has suggested that loss of control and feelings of personal responsibility/inadequacy are the major aspects determining later detrimental effects associated with negative emotional memories. In a recent meta-analytic review of laboratory studies of stress, Dickerson and Kemeny (2004) concluded that lack of control and social evaluation were associated with the most intense and longest duration of arousal. Therefore, the current theory describes the mechanisms by which these aspects enhance detrimental negative emotional memory consolidation.

Cortical System

Unorganized–organized. This dimension refers to the degree to which neural information is integrated and processed. This allows an explanation of the hierarchical arrangement described by Luria (1966) involving primary, secondary, and tertiary cortical zones. Unorganized neural information would be present at the primary receiving areas (i.e., Brodmann areas 1, 2, 3, 17, and 41) and would be reflective of relatively unprocessed sensory information. As neural information moves outward from the primary receiving areas, it becomes more organized such that a single more-organized column represents the activity of two or more (e.g., thousands) of less-organized columns. However, it is speculated that the maximum number of columns projecting to any single column would probably be 7 ± 2 . This is consistent with Miller's (1956) observations on the capacity for processing information across a range

of sensory dimensions. In such a case, one higher-order column's 7 ± 2 input columns can each have 7 ± 2 columns feeding bits of information to them. The higher-order column can then feed its output to an even higher order column. In such a manner, there could a rapid and exponential increase in the number of bits represented by a single column.

Calvin (1995) has noted the existence of both temporary and permanent columns. He notes the relationship between permanent columns and ephemeral entrained pairs whose synchrony is destroyed in an instant by a wave of inhibition. In processing information he describes the probable development of triangular mosaics given that a superficial pyramidal sends axon collaterals in many directions. He notes that two entrained cells may send axon collaterals to an equidistant point, with impulses arriving simultaneously, and so entrain it as well. Moreover, because the basis of recruitment and entrainment is conduction time, not distance per se, various distortions of the mosaic might be seen. He concludes that the largest possible "unit area" without repetitions will be hexagonal in shape.

This maximum pattern of activation (whether the mean is six, seven, or some other relatively low number), would likely be consistent across the entire cortex given the design of columns. This would then limit the maximum amounts (i.e., chunks) of information that are immediately accessible.

This "chunking" of information has been quite a consistent finding regardless of one's expertise. Chase and Simon (1973) provided evidence that experts and novices of chess are able to recall only about seven pieces from randomly generated positions of pieces on a chessboard. However, chess masters are able to recall the pieces on a mid-game almost perfectly after only five seconds of exposure, while the novice can only recall five to seven pieces. The analysis of the experts revealed the extraordinary recall reflects the ability to group four to six memory pieces into a single unit, or chunk. The chess masters have a large knowledge base of common perceptual patterns (i.e., meaningful and well learned) of chess piece positions. Experts appear to be able to recognize such common patterns from past experience, and then the location of the pattern only has to be referenced in long term memory when recalling the pieces. In this manner, it would be possible to have multiple columns, or bits of information, represented by a single cortical column. More recently, chunking of information has been incorporated into an artificial intelligence program design (Moss, Cagan, and Kotovsky, 2004).

The chunks that become consolidated (i.e., columnar arrays comprised of any given column's afferent projections) would be those frequently used or encountered. In a simple test of auditory span, patients hear or read unfamiliar lists of numbers that are immediately recalled. Theoretically, the current model would suggest that the digit columns activated by this task would result in the activation of a single higher-order column. When repeating the list

back, the higher-order column would reactivate its subordinate columns. Without additional exposure to the same number list, there would be little expectation the digits will be consolidated into long term memory. In such a case, when tested a year later there would be little chance of a practice effect. However, the seven digits of one's own phone number are used frequently, resulting in a greater likelihood of long-term memory storage. Thus, many individuals can years later recall their long-ago disconnected phone numbers.

Despite other possible neuronal layer mechanisms involved with columnar control, one specific example will now be presented. Although the example takes into consideration some neuroanatomical data (Calvin, 1995; Carpenter, 1976; Collonier, 1966) concerning the cellular structure of the cortical layers, it is recognized that there are no definitive works on the functional nature of the afferent and efferent connections of these cells, particularly in layer I (Mountcastle, 1997). Therefore, the following example is for heuristic purposes only. It is important to note, however, that similar mechanisms to those described herein are present in the visual processing of the Macaque monkey (Van Essen and Maunsell, 1983).

Layer I horizontal cells may serve to determine the boundaries of the columns, while layer II cells could provide vertical inhibitory control over the neurons contained in the other layers. Layer III cells' axons could provide columnar efferent and afferent activity tied to other cortical areas. Layer IV cells would receive excitatory input from subcortical (including thalamic input) and/or less-organized columns, and neuronal input to this layer would serve to activate the column. Layer V cells could be viewed as providing columnar efferent activity to subcortical regions, and layer VI cells could provide efferent activity to the thalamus.

Given this arrangement of the layer functions, a series of events would occur as follows. Incoming information from subcortical or lower-order columns would enter layer IV causing excitation of the column and all other layers within that column. The initial excitation of layers III, V, and VI would result in columnar output to other cortical and subcortical regions, and followed by inhibition of further efferent activity by the inhibitory influences of cells in layer II. The results of these events would be to excite the column, then to allow excitatory output to other cortical columns and subcortical areas, then to inhibit further output from that column and still have the column remain in an activated state by self re-exciting loops within the column.

Disinhibition of cells in layers III, V, and VI can be controlled via inputs to layer II cells from other cortical columns or subcortical (e.g., thalamocortico) fibers. For example, a more-organized column could reactivate a less-organized column's layer III or layer VI via layer II inhibition in the less-organized column. This would result in an ongoing circuit of activity. Such a

process could explain what is occurring during such acts as "visualizing" in one's mind. For example, a higher-order occipital column can disinhibit lower-order occipital columns and establish a visual circuit.

In like manner, thalamo-cortico projections to layer II or layer IV could disinhibit a given column's layer VI cells that project back to the thalamus. This explains possible cortical column functioning in relation to the previously discussed long term memory loop. General activation of the cortex around the area of a new memory would result in the activation of all the columns associated with the memory, as would be the other columns in that area. The inhibitory fields around the columns of the new memory would strengthen (i.e., "signal") the new columnar array since all but the immediately adjacent or overlapping columns (i.e., "noise") are being activated in the region.

A study of interest in this regard was that of Hempel et al. (2004), in which cerebral activation associated with a visual spatial working memory task was monitored before, during, and after four weeks of daily training. Functional MRI in the nine healthy subjects showed all had a pronounced activation mainly involving the right inferior frontal gyrus and the right intraparietal sulcus. While these regions showed activation increases with improved performance after two weeks of training, the activation values decreased at the time of consolidation of performance gains after four weeks. This would be consistent with the current proposal that thalamo–cortical regional activation would occur to facilitate the new columnar arrays associated with learning the task. However, as the columnar arrays become more firmly established, the general activation is no longer needed.

After learning has occurred, it seems likely that a more-organized column would tonically inhibit certain neuronal output from its associated lower-order columns. For example, after a less-organized column (e.g., representing a given phoneme) has the ability to pass excitatory efferent activity to a number of more highly-organized columns (i.e., all words containing that given phoneme), as well as distal columns, then constraints need to be placed on the less-organized column's output. This would be due to the time required to integrate fully the information coming into the more-organized columns. Therefore, a column's layer III and V efferent activity may be blocked by inhibitory fibers emerging from higher-order columns, while layer IV would receive no higher-order column inhibition since it is required to allow possible activation of those more-organized columns.

If an arrangement of layer functions similar to that described does exist, the size of cortical layers would correspond to the demands placed upon the columns in that cortical region. Therefore, the example presented would fit with the fact that the largest layer IV is present in the primary receiving areas, with fewer layer IV cells being present as the columns are located further away from a primary receiving area.

Simultaneous—sequential. The current model considers parietal lobe functioning to be simultaneous and temporal lobe functioning, particularly anterior and inferior, to be sequential. Frontal and occipital lobe functioning is considered to be a combination of simultaneous and sequential processing. Convergence zones in the posterior cortex would blend the processing types. The closer to the convergence zones, the more blended the processing would become.

As columnar activation occurs within transition areas between parietal, temporal and/or occipital lobes, it seems clear that separate simultaneous and sequential columns could activate a single more-organized column and vice versa. Such a pattern could explain how relational manipulations of information (e.g., syntax, computations) and multisensory processing would occur. In the former case, the sequential characteristics (e.g., the order of words spoken) and the simultaneous characteristics (e.g., the relation of the subject, verb and object of a sentence) of information involve a single cortical column. In multisensory processing, the sensory qualities of sequential (e.g., auditory) and simultaneous (e.g., tactile) stimuli would be represented by a single higher-order column. Novel or infrequently activated columns would be ephemeral.

Sensory-nonsensory. Since this has been adequately explained, the discussion will focus on incorporating this dimension with the others. Of special note are the sequential, multisensory columns of the anterior and medial temporal lobes. The current proposal supports a different view of the temporal lobe and hippocampal involvement than others to date. Consolidation theory (Squire, Cohen, and Nadel, 1984), multiple trace theory (Nadel and Moscovitch, 1997), and relational binding theory (Shimamura, 2002), each support an interplay between the anterior and medial temporal lobe with the posterior association cortex in the consolidation of episodic memories. The current theory agrees there is interplay, but differs in the assertion that the cotico-thalamo-cortico connections are responsible for the consolidation aspect in both the anterior and medial temporal lobe "episodic" memories (i.e., columnar arrays), as well as the "factual" posterior cortical-sensory memories. The frontal lobe memories consolidate in similar fashion, via the reciprocal dorsomedial nucleus connections. Once established, the long term memory arrays in the anterior temporal and more posterior cortex form the complex, personalized memory. The thalamic nuclei may continue to be involved in the memory circuitry during recall of associative aspects of generic and episodic memories (Kraut et al., 2003), though once consolidated, there are likely to be direct connections between anterior/medial temporal (episodic) and the more posterior (generic) columns.

Specific effects are predicted tied to specific damage to the cortex, thalamus, or their interconnecting fibers. For example, the posterior sensory cortex

is connected to the pulvinar nuclei. If the pulvinar nuclei or the interconnecting fibers are destroyed, new "factual/generic" long term memories tied to their respective cortical columns could not occur, though "episodic/personal" memories tied to previously stored factual memories would likely not be affected. If the reciprocal connections between the anterior/medial temporal lobe and the dorsomedial nucleus are destroyed, new episodic memories could not occur, but new factual memories could be formed. This is consistent with the review of human and non-human studies by Aggleton and Brown (2002). If the dorsomedial nucleus is destroyed bilaterally, then new episodic memory formation could not occur. The current theory would also predict impairment in assimilation of rapidly presented information since the frontal connections to the dorsomedial nucleus initiate the posterior thalamic memory formation. This occurs via the dorsomedial nucleus' activation of the intralaminar and pulvinar nuclei. However, any information that does result in activation of the pulvinar and posterior cortical areas would enable long term memory formation. Such activation may be possible by reflexive cortico-thalamocortico circuits associated with repeated stimulus exposure, but would take numerous exposures to accomplish.

The nonsensory (i.e., nonpressure, nonlight) end of the dimension would be represented by the frontal lobes. Evidence would suggest that the prefrontal regions would follow a combination of sequential and simultaneous patterning of columnar activity. The absence of sensory bounds and its simultaneous/sequential patterning, in conjunction with numerous interconnections of the frontal region to other cortical and subcortical regions, is consistent with the neuropsychological data suggesting the frontal region is responsible for the planning and execution stage of higher cortical functions, regardless of sensory mode.

Global–analytical. This dimension relates anatomically to the two cortical hemispheres. Environmental stimuli activate the two hemispheres simultaneously in a parallel fashion and it has been theorized that the side that can most effectively address ongoing requirements is the one that assumes control or initiates cross hemisphere coordinated activities (Hellige, 2002). With the presentation of similar sensory information to each hemisphere, the raw information would be organized, following learning, to be the most usable for the processing in that hemisphere. This selection of useful information would be at a relatively slow pace, developmentally speaking, since the most useful information is determined by behavioral efficacy (e.g., effective environmental control). This would reflect the fact that useful information of a given hemisphere would tend to be consolidated into memory (e.g., form connections from less- to more-organized sensory columns). In contrast, useless information would result in no attention and little probability of memory formation.

As noted by Luria (1966), the primary sensory receiving areas and closely adjoining areas are similar in design across the hemispheres. As the distance increases from the primary receiving areas toward more-organized areas, dissimilar functions are associated with each hemisphere. The current model explains these differences as a function of columnar interconnections. As suggested by Semmes (1968), the right hemisphere appears to involve a more diffusely-organized network of neurons, with the current model going further and suggesting the columns are more diffusely-organized compared to the left hemisphere. This organization would result in the diffuse columnar activation labeled global processing. As previously mentioned, a diffuse arrangement would be important in performing tasks (e.g., emotional analyses, spatial mathematics, novel motor tasks) requiring rapid involvement of distal cortical areas.

The left hemisphere's higher organizational arrangement of interconnecting columns is proximal and more concentrated. This appears consistent with microanatomical asymmetries found in comparing left and right temporal regions (Hutsler, 2003). Other authors (Bradshaw and Nettleton, 1981; Levy, 1969; Russo and Vignolo, 1967) have described analytical processing associated with the left hemisphere. A concentrated, high volume columnar arrangement would lend itself well to the requirements of processing large quantities of finely detailed information. Such behaviors as reading (once well learned), performing rote or rule-governed mathematics, and spelling, would require an analytical arrangement.

Support for the proposition that negative emotional memories are stored in the right posterior lobes comes from several studies. Metzger et al. (2004) reported increased right parietal EEG activity associated with post traumatic stress disorder arousal symptoms. An fMRI study comparing small animal phobics with non-phobic controls revealed significantly greater right insular cortical activity when viewing fearful versus neutral faces (Wright, Mantis, McMullin, Shin, and Rauch, 2003). In a single positron emission computed tomography and MRI study (Bonne et al., 2003) of recent (six months) post traumatic stress disorder patients compared to controls, increased resting state regional blood flow differences were noted for the patient group in the right precentral, superior temporal, and fusiform gyri. In a neuroimaging study, Rauch et al. (1996) evaluated individuals with a post traumatic stress disorder. Results showed that script-driven imagery led to increased activation of the right secondary visual, temporal, insular, and orbitofrontal cortex, as well as the right amygdala. There was also a decrease in the left hemisphere speech production region.

From a logical level, it seems reasonable that the right hemisphere would be involved in negative emotional processing. First, responses to environmental threats require quick responses, which are best accomplished by the purport-

ed global processing of the right hemisphere. Additionally, verbal and nonverbal emotional expressions are relatively undetailed (e.g., loudness and abruptness of onset of speech, fearful or angry facial expressions), similar to music sounds. The current theory has suggested that faster, less-detailed processing is performed by the right cortex. This is similar to the conclusions of Tervaniemi and Hugdahl (2003) who reviewed recent findings and current views about the structural and functional basis of human brain lateralization in the auditory modality. They note that the human brain has a strong predisposition to process speech sounds in the left and music sounds in the right auditory cortex of the temporal lobe (most notably the planum temporale). They note the predisposition is not bound to the informational sound content, but to the rapid temporal information more common in speech than in music. By rapid temporal information, they are describing higher volume of information analyses required in speech.

The rich interconnections of hemispheres clearly suggest that the hemispheres engage in frequent exchange of neural information. Such exchange can be both excitatory and inhibitory. However, any given frontal attention center of a hemisphere would be limited to accessing information within its respective posterior hemisphere via the intrahemispheric tracts. There are no major tracts connecting the frontal area of one hemisphere to the posterior area of the other. Thus, the left frontal lobe (i.e., verbal, analytical) cannot directly access and manipulate non-verbal emotional memories purported to be stored in the right posterior cortex. Consistent with this view, Gazzaniga (2002) notes that split brain research has demonstrated that the verbal "interpreter" of the left hemisphere will give explanations regarding emotional experiences tied to the right hemisphere, although these explanations may well be erroneous.

As previously stated, whichever hemisphere first arrives at a solution when being presented with a problem, that side's frontal area would assume control over the ensuing response. Simultaneously, there should be an inhibition of the behavioral expressions of any solutions from the opposing hemisphere's frontal area provided the ongoing behaviors are being effective in solving the problem. This would be necessary to prevent the opposing hemisphere from initiating its own solution that might conflict with that of the controlling hemisphere. Obviously, if feedback to both hemispheres indicates the controlling hemisphere's behavioral response is being ineffective, the inhibitory control can be discontinued and the other hemisphere has equal opportunity at controlling further responses. Similar to this pattern, coordinated cross-hemisphere tasks would require an alternating pattern of activation and inhibition of the frontal lobes. In such a case, one column of a hemisphere would serve as the initiator or driver of the ensuing activation and inhibition of less-organized columns (i.e., a decoding process).

Similar to emotional responses that can occur without a verbal thinking process, other activities involved with the right hemisphere can occur. Motor responses and melody reproduction can occur with no verbal thinking activity. In such a case, neural information is integrated (i.e., less- to more-organized) in the right posterior hemisphere and then behavioral responses are programmed by the right frontal area. Thus, it is clear that the current model considers right hemisphere activity to be equally as conscious as left hemisphere processing, though the right hemisphere is basically non-verbal (noting the exception of some lyrics housed within music analysis and reproduction and words strongly associated with the expression of emotions, such as profanity). Thus, the terms "conscious" and "unconscious" are meaningless within the context of this deeper understanding.

Motor system. The motor system represents the manner in which the brain can effectively interact with the environment. Any movement, including verbalization, will require the production and regulation of multiple motor neurons that project fibers through the corticospinal tract. This would suggest that the regulation of movements would occur prior to the final cortical neuronal discharges to the spinal motor neurons.

The motor system would become involved following sensory information processing in the posterior cortex and the formulation of a sequential plan of action by the nonsensory/sequential/simultaneous cortical columns of the frontal lobes. Intrahemispheric cortical input to the columns of the premotor cortical areas would be the first stage of any given behavioral response. Columnar output from the premotor cortical regions to the striatum and cerebellum would follow. Such a possibility would appear consistent with Doyon and Ungerleider's (2002) discussion of motor skill learning.

Developmental Aspects

The discussion will now focus on the implications of certain developmental patterns of the present model. The first implication involves global versus analytical memory formation during the developmental period. In this regard, more-highly-organized memories would have to occur first in the right hemisphere given the purported diffuse design of columns. As such, any cortical functions that require undetailed analysis would be the first to occur. This obviously includes emotional processing and expression. As such, it would be expected that the emotional memories occurring during the first two years of life, and perhaps longer given the myelination patterns described below, would not have any means by which verbal labeling could occur. In explanation, the left hemisphere would still be at a level of analyzing and subsequently reproducing phonemes (i.e., learning to talk) while the first emotional memories are being stored.

An important post-natal developmental pattern exists in relation to the myelination of interhemispheric and intrahemispheric tracts that connect cortical regions. Specifically, myelination of these tracts continues through adolescence and possibly adulthood (Lenneberg, 1967). The lack of myelination would severely limit the amount and speed of information exchange among the connected areas. The existence of such limitations in interhemispheric connections is supported by findings of asymmetrical event related potentials in EEG's of children (Rourke, Bakkar, Fisk, and Strang, 1983).

The lack of myelinated connections between distal cortical regions at an early age may be important in allowing the independent development of each cortical region. For example, interhemispheric transfer of information that occurs too early would detrimentally influence the initial organization of raw input in each temporal region. The lack of cross communication would allow the hemispheres to develop their own independent analysis of auditory input, which seems logical for the most efficient functioning of the organism. After the more-organized cortical areas of each hemisphere (or lobes within hemispheres) have developed, then the less-organized areas could initiate "cross talk" with no compromise in independent analysis of information. Along these lines, actual interhemispheric connections (i.e., axonal sprouting and dendritic spine increases) between cortical columns would follow a similar developmental pattern.

If these latter points are correct, then interhemispheric columnar connections would be expected to follow a specific pattern. This would involve lower-order columns of one hemisphere being interconnected with lower-order columns of the other hemisphere. Higher-order columns should follow the same pattern. The result of such a developmental sequence on recovery of function after a localized lesion should be as follows.

Following the development of higher-order columns and their interhemispheric connections, damage only to the primary receiving area of one hemisphere would have little effect on higher-order columns. This would be due to the interhemispheric transfer between the slightly more-organized columns (e.g., Luria's secondary analyzer zones) that convey partially-organized information (i.e., compensation for the loss). However, if more-organized columns are also damaged in a hemisphere, then the more-highly-organized columns in the hemisphere would be unable to process the sensory information conveyed from the other hemisphere, even in the presence of intact interhemispheric connections between the intact higher-order columns. This would be due to the need by the damaged hemisphere's higher-order columns to use their lower-order columns to integrate and interpret specific sensory information. When able to use an alternate sensory mode within the same hemisphere, however, the higher-order columns become accessible and interpretable. This modality-specific nature of a given sensory modality's higherorder columns provides an explanation for the various sensory agnosias.

If the developmental aspects of interhemispheric communication are considered, an explanation is possible for the recovery of auditory—phonemic processing in some young children with temporal lobe damage. In this regard, if damage is restricted to the primary receiving or slightly more-organized areas of the left temporal lobe, then the potential "phoneme" columns of the right hemisphere would provide input to the same corresponding location in the left hemisphere. Such recovery of function would occur at the time that the interhemispheric myelination, and possible neuronal growth, became more complete between the two regions. However, if damage to the left hemisphere occurred in the region containing the future or existing "phoneme" columns, then no recovery of spoken language comprehension would occur.

The current model strongly supports the role of learning on neuronal growth patterns and the need for lower-order column development for higher-order columns to function. Given the data (Berg, 1984) that synaptic target tissue use is not only a major determinant of new neuronal growth, but may also be a major factor in neuronal survival (i.e., unused neurons may die), then the influence of early development of higher-order columns becomes obvious. As previously suggested, the initial development of higher-order columns is dependent upon excitation of primary sensory columns. Early rich environmental stimulation would lead to an increased number of higher-order columns developing, while impoverished environmental stimulation would not. Thus, higher-order columns may be unable to develop later due to massive neuronal death in the "association" cortex. This may be the process leading to the development of socio-cultural mental retardation.

The applications of the current model to psychotherapy integration and treatments is beyond the scope of the current paper, but has been discussed elsewhere (Moss, 2001, in press). In this regard, it represents a step away from the three main orientations in psychotherapy (i.e., psychodynamic, humanistic/existential, and cognitive behavioral) into one based on an actual brain model. This model is used to explain to the client the development of psychological problems, as well as why specific treatment approaches would be expected to result in desired improvements.

Conclusions

The current paper has proposed cortical memory to be a function of interconnecting cortical columns. However, the true value of this model will await a priori studies based on predictions made by the model. An obvious criticism of the proposed model has to do with its testability. However, there are two developments that may make the model testable in the foreseeable future. First, there is developing technology that may allow direct assessment of cortical column activity. Kim and Duong (2002) have reported on the use of fMRI techniques in the mapping of submillimeter columnar structures in a noninvasive manner. However, it is unclear whether such techniques will be able to differentiate overlapping columns, if these do indeed exist.

The second exciting development has been termed the *Blue Brain Project* (Giles, 2005). This project is using computer modeling of neurons and cortical columns on the eighth fastest supercomputer in the world. The goal is to produce a working brain model. Thus, it would appear that the time is ripe for even speculative models of cortical functioning since the technology will soon exist to determine the feasibility of such models. It is hoped that the current paper, though speculative, will serve as a productive step in our understanding the physiological basis of learning and memory.

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