

## MANAGEMENT OF NEOCORTEX RESOURCES AS THE PRIMARY ROLE OF THE HIPPOCAMPAL SYSTEM

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### ABSTRACT

A model is described in which the hippocampal system functions as resource manager for the neocortex. This model is developed from an architectural concept for the neocortex in which the receptive fields of cortical columns can gradually increase but with some narrowly defined exceptions cannot decrease. The definition process for receptive fields is constrained so that they overlap as little as possible, and change as little as possible, but at least a minimum number of columns detect their fields within every sensory input state. Below this minimum, the receptive fields of some columns are increased slightly until it is reached. The columns in which this increase occurs are selected by a competitive process in the hippocampal system that identifies a group of columns for which only a relatively small increase is required, and sends signals to those columns that trigger the increase. These increases in receptive fields are the information record which forms the declarative memory of the input state. Episodic memory associates all columns in which receptive fields increased simultaneously, and the hippocampal system is therefore the appropriate source for information guiding access to such memories. Semantic memory associates columns which are often active (with or without increases in receptive fields) simultaneously. Initially, the hippocampus may guide access to such memories on the basis of initial information recording, but frequent access shifts control to other parts of the neocortex. The roles of the mammillary bodies, amygdala and anterior thalamic nucleus can be understood as modulating information recording in accordance with various behavioral priorities. Provisional physical connectivity created during sleep supports receptive field increases in the subsequent wake period. Previously created memories are not affected. This model matches a wide range of neuropsychological observation better than alternative hippocampal models. The neuron mechanisms required by the model are consistent with known neuron physiology.

### INTRODUCTION

Since the observations of the combination of memory deficits in patients after surgical removal of parts of their hippocampal system [31], there has been strong interest in the role of this structure in memory. However, these and subsequent observations showed three dissociations which have presented challenges to understanding the actual role of the hippocampal system. One is that although there can be severe

anterograde amnesia for both semantic and episodic memory, retrograde amnesia is stronger for episodic memory. The second is that speech capabilities, general intelligence, and previously acquired skills are unaffected, despite the memory deficits. The third is that although the ability to create new declarative (i.e. semantic and episodic) memories is strongly affected, a significant ability to learn sensorimotor skills is retained. These dissociations have been demonstrated, for example, in the extensively studied patient HM [e.g. 8].

Furthermore, lesions to structures such as the mammillary bodies of the hypothalamus and the anterior thalamic nuclei can generate similar combinations of deficits in the absence of damage to the hippocampal system. Thus damage to the mammillary bodies of the hypothalamus can result in anterograde memory deficits [34], damage to the anterior thalamic nuclei can result in both anterograde and retrograde amnesia [6], but again in such cases all other cognitive capabilities are unaffected. It has also been observed that the amygdala plays a role in enhancing the memory of emotional events [28]. A wide range of functional roles have been proposed for the hippocampal system to account for the observed combination of deficits. Many of these models propose two component systems to account for the combination of global anterograde semantic and episodic amnesia with stronger retrograde episodic amnesia. Typically these models have a component supporting stimulus memory and a component supporting episodic retrieval [e.g. 19], and argue that detailed stimulus information is initially registered in the hippocampal system and gradually transferred to long term storage in the neocortex. The models in general have issues in providing an account for the full range of experimental observations [7], and do not provide any functional reason for the roles of the mammillary nuclei, anterior thalamic nuclei and amygdala other than speculation about possible redundancy [e.g. 20].

An alternative concept provides an intuitively simple reason for the existence of the hippocampal system, eliminates the need for information transfers back and forth between neocortex and hippocampus, and provides straightforward reasons for the existence of the various dissociations. The concept can provide an integrated account for the role of different parts of the hippocampal system, the anterior thalamic nuclei, the mammillary bodies and the amygdala in memory. In addition the required functional processes can be mapped to

plausible neuron processes. Finally, it includes a memory related role for sleep including dream sleep that is more consistent with experiment that the alternative memory consolidation models.

This concept is that the primary role of the hippocampal system is management of the information recording resources of the cortex. A major part of this role is determining at each point in time where information about current sensory inputs will be recorded in the neocortex, performing this function by managing a competition between all cortex areas to determine the most appropriate combination of locations. A side effect of this function is that the hippocampal system acquires information about which cortex areas record information at the same time, information critical for episodic memory retrieval and navigation. Retrieval of semantic memory, on the basis of associations between cortex areas frequently active at the same time, becomes independent of the hippocampal system. The role of sleep includes configuration of neocortex resources to be appropriate for recording information in the immediate future, using past experience (with a bias in favor of the most recent) as the best available estimate for future experience.

**THE RESOURCE MANAGEMENT MODEL OF HIPPOCAMPAL SYSTEM**

As pointed out by [26], a full theory of the hippocampus must link processes at molecular, cellular, network and behavioural levels. A critical element in such a theory is some concept of what information processes the hippocampus contributes to the brain and to the neocortex in particular. Such a concept requires a system architecture of the brain as a whole. A general system architectural model of the brain has been proposed by [9, 11, 12, 13]. Theoretical arguments have been offered that any system which must learn a complex combination of behaviors with limited information handling resources will be constrained into the forms of this model by a number of practical considerations [10, 11, 12, 13].

The general architectural form of the model is illustrated in figure 1. The greater the ratio of behaviors to resources, the more tightly the system will be confined within this architectural form [10, 11, 12, 13]. As illustrated in figure 1, there are a number of separations between subsystems which perform different types of information processes, and evidence from physiological structure, dissociations between different cognitive processes, and the deficits resulting from local damage has been offered [13] to support the view that there is a correspondence between these subsystems and the physiological structures of the mammal brain.

In the model, a pyramidal neuron in the cortex detects a group of similar information conditions. Each condition is a combination of simpler conditions (or of raw sensory inputs). A condition is defined by a group of inputs communicating the detection of simpler conditions by pyramidal neurons in an earlier cortical layer. The inputs defining each condition are separately integrated by an arm of the dendritic tree. If the condition is present, integration across the arm is large enough to inject postsynaptic potential deeper into the dendrite. If the total potential injected into the dendrite exceeds a threshold, potential is injected into the soma that causes the neuron to fire. In information terms, such firing indicates the detection of a

significant proportion of the conditions programmed on the neuron. The receptive field of the neuron is defined by the group of conditions which it detects.

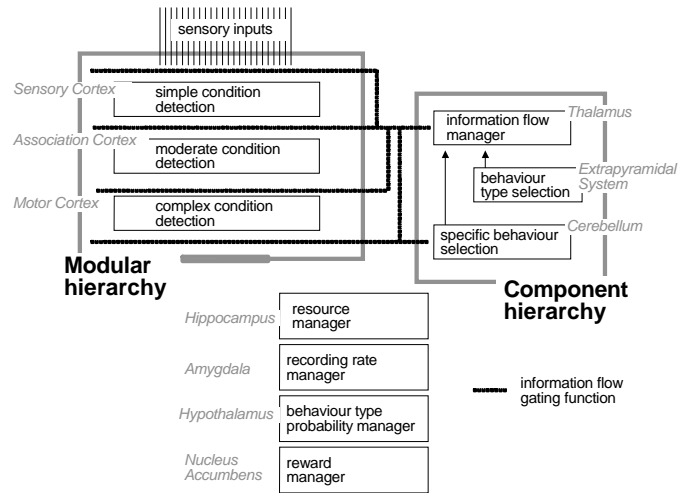
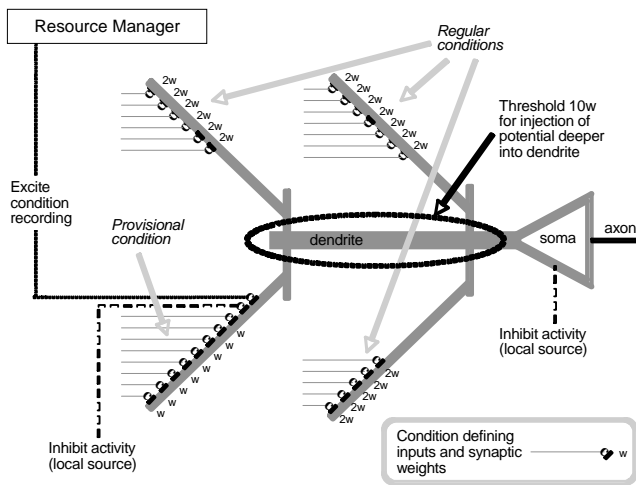


Figure 1. The architectural form into which a system will tend to be constrained if it must learn a large number of different behaviors with limited resources is illustrated. The modular hierarchy defines and detects conditions within the information available to the system. Many condition detections flow to the component hierarchy where they are interpreted as recommendations in favor of a wide range of behaviors. The component hierarchy selects and implements the most strongly recommended behaviors. Reward feedback acts upon the component hierarchy to change recommendation weights but cannot change condition definitions. Decisions on where to record conditions in the modular hierarchy at each point in time are made by the resource manager on the basis of inputs from the modular hierarchy. Selection of a general type of behavior can be influenced by general circumstances via the behavior type probability manager. Such selections include influencing the rate of condition recording. Special circumstances can also result in elevation of the rate of condition recording by the recording rate manager. The brain structures corresponding with these subsystems are indicated in italix [12, 13].

New conditions can be added to a neuron using provisional conditions. As illustrated in figure 2, a provisional condition is a group of inputs indicating the detection of simpler conditions, plus management inputs indicating in information terms that recording of regular conditions is appropriate, all on the same separately integrated dendritic arm. The condition detecting inputs initially do not have enough total synaptic strengths to inject potential from the arm into the dendritic tree. However, if many of these condition detecting inputs are active, and the management input is also active, the total synaptic strength is sufficient. If in this situation a number of previously programmed conditions are also present, there may be enough input to cause the neuron to fire. If the neuron fires, a backpropagating action potential increases the synaptic strengths of the recently active provisional inputs, so that they can in the future contribute to the firing of the neuron independent of the state of the management inputs. In information terms, a new condition has been recorded. This algorithm is essentially the well known LTP mechanism [5]. Use of the algorithm as described allows slight expansion of the neuron receptive field under appropriate circumstances.



**Figure 2. Information model of pyramidal neuron. For explanation see text.**

In the architectural model, the cortical column made up of pyramidal neurons arranged in (generally) three layers is the primary functional unit in the cortex, and has two roles. One role is to indicate the presence of a significant proportion of the conditions programmed in the column (i.e. detecting a receptive field). This receptive field is a composite of the receptive fields of the column pyramidal neurons. Such a detection by one column is interpreted by subcortical structures as a set of recommendations in favour of a wide range of different behaviours, each with a specific weight. The subcortical structures determine the behaviour with the largest total weight across all columns detecting their receptive fields, and implement that behaviour [9, 11]. At least a minimum number of columns must detect their receptive fields in response to each sensory state, to ensure a range of recommendations adequate to generate a high integrity behaviour.

The other role of a column is to determine the circumstances in which condition recording (i.e. receptive field expansion) is appropriate for the neurons in the column. Recording is generally appropriate if the total number of active columns is below the required minimum, and appropriate for a specific column if a fairly small expansion of its receptive field will result in an output. The limitation to receptive field expansion is to limit undesirable effects on the integrity of existing recommendation strengths associated with detection of the current field [11, 12]. As described in [11, 12, 13] the column structure is effective for determining expansion appropriateness. To give a simple example, suppose that in a three layer column, the first layer detects conditions that are combinations of column inputs. The middle layer detects conditions that are combinations of the conditions detected by the first layer. The third layer detects conditions that are combinations of conditions detected by the middle layer. Third layer detections are the outputs from the column that are interpreted as behavioural recommendations. If there are significant numbers of condition detections in the middle layer but no outputs from the third layer, the implication is that the column input state is fairly similar to states which have resulted

in a column output in the past, and slight expansion of the column receptive field may be appropriate.

A competition is therefore required between all columns on the basis of degree of middle layer activity to determine which columns are the most appropriate locations for condition recording. If middle layer activity is very strong, column output is probably also present and recording less appropriate. Such a competition could be implemented by all-to-all connectivity between columns, but use of connectivity resources will be much more efficient if the competition is handled by a central resource manager. This manager will receive inputs ultimately from every column, perform the competition, and send outputs back to the winning columns which form the condition recording management inputs described earlier. Computer simulations have demonstrated that a set of columns using this competitive process can self organize to discriminate between input states with behaviourally different implications [11, 18].

The primary role of the hippocampal system in the resource management model is to select the cortical columns that will record information at each point in time. It performs this role by (i) collecting information on the degree of activity in each cortical column, (ii) processing this information to determine the relative activity of different (partially overlapping) groups of columns that have tended to record information at similar times in the past, (iii) performing a competition between the groups to determine the appropriate locations for recording, and (iv) generating outputs to appropriate pyramidal neurons that drive the recording. Competition on the basis of groups of columns makes use of information about past recording and improves the probability of selecting the most appropriate set of columns for current information recording.

Various structures including the thalamus, hypothalamus and amygdala act upon the hippocampal system to modulate the selection of the appropriate cortical columns and the overall degree of condition recording. The amygdala increases the degree of condition recording above the base level in strongly emotional circumstances. In information terms, this reflects the probability that such circumstances may be more useful than average for guiding future behaviour, justifying extra information recording. The hypothalamus biases information recording in favour of cortical areas which tend to generate recommendations in favour of different general types of behaviour (aggressive, food seeking etc.). The bias is one way in which the probability of selection of a behaviour of the type is increased. The thalamus received recommendations in favour of condition recording on the basis of the value of such recording in different past experiences, and applies those recommendations to the hippocampus.

This model of the resource manager can be understood by consideration of the major physiological connectivity routes as illustrated in figure 3. In the model, information on the internal activity of cortical columns (i.e. activity of pyramidal neurons in an appropriate layer) is communicated to the parahippocampal and perirhinal cortices. Receptive fields of columns in these cortices are groups of columns that have recorded information in the past at the same time. Outputs from one layer of these parahippocampal and perirhinal columns target the cortical columns providing their inputs, and constitute the condition recording management inputs to those columns.

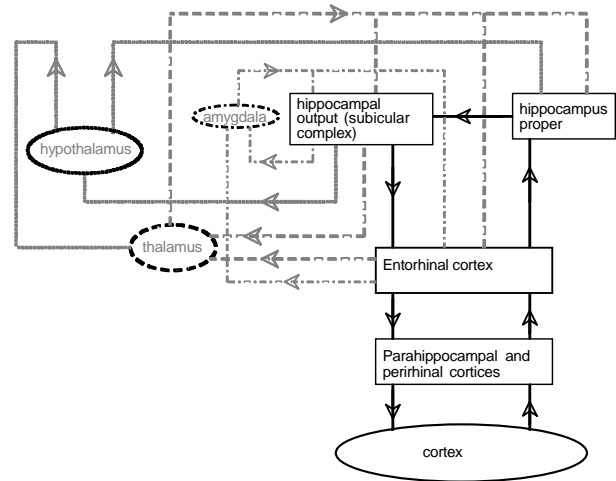
These outputs are not activated without inputs derived ultimately from the hippocampus. Outputs from another layer of parahippocampal and perirhinal columns target the entorhinal cortex. In the entorhinal cortex, columnar receptive fields resulting from these parahippocampal and perirhinal inputs are groups of groups of cortical columns that have recorded information at the same time in the past. Entorhinal columnar outputs from one layer target the parahippocampal and perirhinal columns providing their inputs, and constitute the condition recording management inputs to those columns. These outputs are not activated without inputs derived ultimately from the hippocampus. Entorhinal outputs from another layer are provided to the hippocampus proper, i.e. CA fields and dentate gyrus (DG). A high level of entorhinal input thus indicates that the current input state is relatively familiar, and a low level of condition recording is appropriate. Conversely, a low level of entorhinal input indicates a novel situation, requiring a high level of condition recording. A competition occurs within the hippocampus proper to determine the groups of columns most appropriate for recording information, and the hippocampal output structure (the subicular complex) begins the conversion of the outputs of this competitive process into signals that can drive recording. This conversion process continues back through the associated cortices to the cortex proper.

The hypothalamus acts on the hippocampus to bias the competition in favour of certain cortical areas. The amygdala acts on the output structures to increase the volume of recording in specific areas if appropriate. The thalamus acts on both the hippocampus and the subicular complex to modulate the location and degree of condition recording in accordance with behavioural consequences of past episodes of condition recording.

The competition process can be understood by consideration of figure 4. Input from the entorhinal cortex comes into granule cells in the DG. These cells detect conditions that indicate activity of groups of groups of groups of cortical columns, and have two types of target in area CA3. Firstly, they excite specific structures on the dendrites of CA3 pyramidal neurons with similar receptive fields to the source granule cells. Secondly, they excite CA3 interneurons that inhibit a wider range of CA3 pyramidal neurons with different receptive fields from the source granule cells. CA3 pyramidal neurons have excitatory inputs from both the entorhinal cortex and the DG, and also large numbers of excitatory inputs from other CA3 pyramidal neurons. CA3 pyramidal outputs target granule cells in the DG, and also CA1 pyramidal neurons.

If there is strong input from the entorhinal cortex, the implication is that the input situation is familiar and little information recording is required. In this situation, granule cells will be strongly excited, generating strong CA3 interneuron activity which will prevent significant CA3 pyramidal activity. If entorhinal cortex input is weak, there will be relatively weak activity by granule cells, and weak activity of CA3 interneurons. Initial CA3 pyramidal activity is driven by inputs from the entorhinal cortex and indicates detection of the activity of groups of groups of groups of cortical columns. Direct input from granule cells triggers recording of additional conditions. Feedback from other CA3 pyramidal neurons biases activity in favour of groups of groups of groups that recorded

information at the same time in the past. The effect is to activate a population of CA3 pyramidal neurons corresponding with a set of groups of groups of groups of cortical columns that have all tended to record information at the same time in the past. Condition recording on the CA3 pyramidal neurons will slightly expand their receptive fields to include groups about to record information at the same time. As CA3 pyramidal activity increases as a result of condition recording, feedback to DG granule cells increases, resulting in condition recording on those granule cells, and the resultant increased activity of the granule cells increases the inhibition back into CA3 and limits the buildup of CA3 activity. The larger the input from the entorhinal cortex, the smaller the total CA3 activity. In other words, CA3 activity will be proportional to the degree of novelty in the current input state.

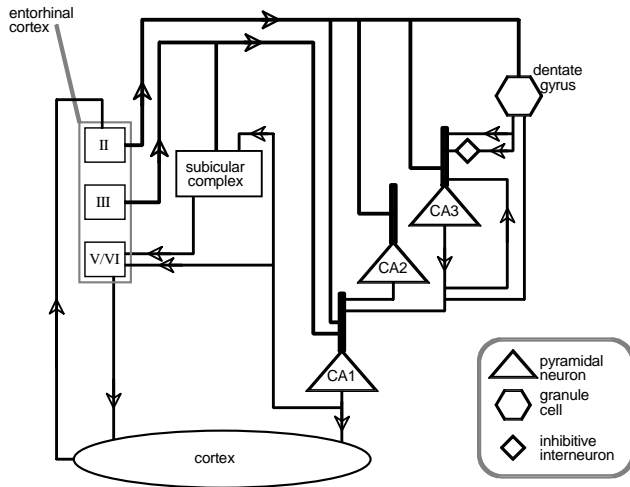


**Figure 3. Connectivity routes between hippocampal system structures. For connectivity between cortex and hippocampal system see [23]. For amygdala see [21]. For hypothalamus see [3]. For thalamus see [32].**

CA1 pyramidal neurons receive inputs from the entorhinal cortex and detect conditions that indicate activity of groups of groups of groups of cortical columns. Outputs from CA3 pyramidal neurons target CA1 pyramidal neurons with similar receptive fields, and both directly excite those pyramidal neurons and form their condition recording management inputs. CA1 pyramidal neurons thus take the results of the CA3-DG competitive process and generate stable outputs that drive condition recording throughout the cortex.

The first step in this condition recording process is that CA1 outputs target the columns in the entorhinal cortex from which they derive their inputs. Condition recording in the entorhinal columns which occur most frequently in the inputs to the active CA1 pyramidal neurons therefore receive strong inputs. These strong inputs trigger both condition recording and the generation of outputs from the entorhinal columns. The outputs are targeted on the perirhinal and parahippocampal columns which occur most frequently in the inputs to the active entorhinal cortex columns. A similar process results in condition recording in and output generation from the most heavily targeted perirhinal and parahippocampal columns. In turn, condition recording and output occurs in the cortical columns that occur most frequently in the inputs to the perirhinal and parahippocampal columns.

Note that this process results in columns in the entorhinal, parahippocampal and perirhinal cortices expanding their receptive fields to include the new groups of cortical columns about to record information at the same time.



**Figure 4. Detailed view of connectivity within the hippocampus. For connectivity between entorhinal cortex and hippocampus and between CA fields, see [22]. For feedback within CA3 see [4]. For connectivity between dentate gyrus (DG) and CA3 see [1].**

As discussed in [11, 12, 13] any behaviours generated by the enhanced cortical column activations will be followed by some kind of consequence feedback, which will adjust the recommendation weights of the active columns in favour of the selected behaviour. Other recommendation weights will not be affected, but will in general retain their integrity because the changes to receptive fields are small. The hippocampal system thus manages the recording of information in response to sensory inputs in such a way that new information has limited effects upon the performance of previously learned behaviours.

This primary role results in the collection of information which makes the hippocampal system useful for a number of secondary roles. One such secondary role is providing information about groups of columns that have recorded information at the same time in the past, to permit indirect activation of columns on this basis. This type of indirect activation is the mechanism for accessing episodic memories [13, 14]. Another role is supporting navigation, because navigation, like episodic memory, depends on indirect activation on the basis of temporally correlated past recording. A further role is determining the novelty of an experience, on the basis of the overall demand for condition recording.

However, semantic memory involves associating columns often active (generally without condition recording) at the same time [13, 14]. Retaining the required information in the hippocampal system would confuse its primary role, and the function therefore shifts to other cortical areas.

Provisional conditions are required to make the creation of permanent conditions possible. Connectivity sources could be assigned randomly, but the required resources can be reduced and the probability that a provisional condition will be useful increased by biasing the definition of provisional conditions in favour of groups of inputs from columns that have often

recorded conditions at the same time in the past. This can be achieved by taking the brain “off-line” by sleep, and performing a rerun of a selection of past experience, with a bias in favour of recent experience as the best indicator of future experience. Provisional conditions would then result from neurons accepting provisional inputs from sources often active when the neuron itself was active. In simulations this mechanism significantly reduces the connectivity requirements [10]. The hippocampus is the appropriate source of information to guide such a rerun.

### EVIDENCE FOR HIPPOCAMPAL SYSTEM AS THE CORTEX RESOURCE MANAGER

The striking combination of cognitive symptoms associated with damage to the hippocampal system find a natural account in the resource management model. The loss of ability to create new declarative memories results from the loss of the mechanism for selecting the cortical columns in which new information will be recorded and for driving that condition recording. Because all existing columns and their associated recommendation strengths are preserved, there is minimal disruption to most other cognitive capabilities. However, because episodic memory is dependent upon indirect activation of columns on the basis of temporally correlated past recording, and information on such past recording is preserved in the hippocampal system, because the hippocampal system acquires information identifying groups of columns that recorded conditions at the same time in the past in the course of its resource management role, hippocampal system damage results in some loss of such memory. Information to identify groups of columns on the basis of frequent past simultaneous activity or recent simultaneous activity must be collected to support semantic memory and priming. There is no reason for the resource manager to be used for such collection and damage to the resource manager will not therefore affect these types of memory. Recommendation weights of existing columns could still be changed by reward feedback. If a skill could be acquired without changes to column receptive fields, learning could proceed despite hippocampal damage.

Each pyramidal neuron in CA3, CA1, and the associated cortices preserves information identifying groups of cortical columns that have recorded conditions at the same time. The number of columns in the groups decreases from CA3 and CA1 to the entorhinal cortices and decreases further in the parahippocampal and perirhinal cortices. This information is needed for indirect activations in support of episodic memory. However, because outputs from CA1 drive condition recording, the use of CA1 for such a purpose could result in inappropriate condition recording.

Consistent with this understanding, in human subjects damage to CA1 alone generates anterograde amnesia but little if any retrograde amnesia, and no signs of significant cognitive impairment other than this loss of memory (e.g. patient GD [30]). When damage extends to other hippocampal formation structures, retrograde amnesia becomes significant in addition to anterograde amnesia (e.g. patients LM and WH [30], patient HM [8]).

In the resource management model, information derived from sensory experiences is recorded immediately in columns in the neocortex, and subsequent damage to the hippocampal

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system will not affect the information. The only effect of such damage will be on the capability to access such information on the basis of past temporally correlated information recording. If the basis for activation shifts over time towards temporally correlated activity, access will become more and more independent of the hippocampal system. For example, when a word is first learned, there will be information recording in auditory columns activated in response to hearing the word, and in visual columns activated in response to the object or concept of the word. The capability to understand the word depends upon the recorded information and in the short term, actual understanding of the word exist because the auditory columns indirectly activate the visual columns on the basis of simultaneous past information recording, utilizing information from the hippocampal system. After a number of occasions on which the word has been understood in this way, the auditory columns will acquire the ability to activate the visual columns on the basis of frequent past simultaneous activity, supported by connectivity paths within the neocortex and independent of the hippocampal system. To the degree to which this has occurred, access to the information would be expected to result in the most severe retrograde amnesia for episodic memories, less for personal semantic memories and semantic memories of public events and persons, and least for general semantic memory. This graduation is consistent with the observed amnesias [27].

An autobiographical memory is the record of complex, unique events. The link between the information active at the time of the event will therefore be temporally correlated information recording across a complex population of cortical columns, and there is no reason for these columns to be frequently active at the same time. At the other extreme, a new word is the record of a relatively simple link between auditory columns and visual columns and the columns are active at the same time each time the word is used. A shift to information access on the basis of frequent past simultaneous activity is likely to be rapid. The association between the names and faces of public individuals, and personal semantic facts represent an intermediate state. The observed graduation in retrograde amnesia with hippocampal system damage from most severe for autobiographic to negligible for word knowledge is as expected by the model. An exception could be if a particular memory were very frequently described. In such a case, frequent repetition could result in some ability to access the memory independent of the hippocampal system on the basis of frequent past simultaneous activity.

Regular autobiographical memory does not become independent of the hippocampal system. In the experiments of [29], the activation of the hippocampal formation was observed during retrieval of both recent and remote autobiographical memories, and activity was greater for remote memories. In these experiments, the research design stressed depth of recall and encouraged visualization of details. Thus subjects were asked “Can you recall a specific high school teacher?” or “Can you recall the school yard of your elementary school?”, but it was stressed to participants that the questions were meant to cue an actual episode, such as “The time the English teacher brought in a recording of Hamlet and made us listen” rather than a series of facts (like the name of the teacher). Follow-up questions like “Do you recall a time when you were playing in

a specific area of the school yard?”. This design aimed to exclude facts recall and recall of highly salient emotional events (e.g. weddings, graduations, loss of a pet) which may be more common in autobiographic self reports.

Further evidence on the relative roles of CA3 and CA1 comes from the rat experiments of [15]. They used lidocaine to selectively block the activity of CA1 and CA3, and interpreted their results as being consistent with the view that “the CA3 area [acts] as an autoassociative memory network and the CA1 area as a critical output structure”.

In the resource management model, CA1 pyramidal neurons correspond with groups of neocortex columns that have frequently recorded information at the same time in the past. CA3 pyramidal neurons also correspond with such groups, but have interconnectivity with many other CA3 pyramidal neurons corresponding with groups that have recorded information at the same time in the past, but somewhat less frequently. The entorhinal cortex brings together the inputs from such groups and provides inputs indicating the activity in the groups to the hippocampal formation. The entorhinal cortex also receives outputs from the hippocampal formation and translates them back into outputs directed to the individual columns to drive information recording. Hence a mapping between groups of cortical columns that have recorded information at the same time and individual pyramidal neurons can be expected in CA1, CA3, and the entorhinal cortex.

One situation in which recording of information at the same time can be expected is in navigation, where simultaneous recording across a specific population of cortical columns can be expected when in the same location. Pyramidal neuron “place cells” which are active when a rat is in a specific location have been observed in CA1 and CA3 fields [25] and in the entorhinal cortex [17], but not in the more peripheral areas of the hippocampal system [17]. This distribution of place fields is as expected by the model.

Furthermore, given that the role of CA3 is to focus CA1 on an optimal group of columns to record information at the same time, place fields developed in the absence of CA3 would be expected to be less sharp, and changes to the environment would be expected to result in greater changes to CA3 than CA1 place fields, as observed by [24].

In the model, the role of the hypothalamus is to influence current information recording in favor of current general behavioral priorities. Loss of this function would be expected to affect the ability to record information in the future, but to have no effect on access to past information on the basis of temporally correlated past recording. Consistent with this interpretation, damage strictly limited to the mammillary bodies (bilaterally) results in anterograde amnesia but minimal retrograde amnesia [34]. The thalamus influences the level of hippocampal system outputs in general, and damage to the anterior thalamic nucleus can therefore result in both anterograde and retrograde amnesia as observed[20].

In the resource management model, the role of the amygdala in memory is to adjust the degree of hippocampal system driven information recording during emotional events in favor of cortical areas where the increased recording is likely to be useful in determining behavior in the future. Consistent with this role, it is found that emotional arousal biases the memory of the event in favor of the gist and reduces the memory for

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visual details, and that bilateral damage to the amygdala eliminates the bias [2].

In the model, one role of sleep is to configure provisional conditions, with REM sleep providing a partial rerun of past experience to guide condition definition. Correlations between neuronal activity during waking and during the subsequent sleep period have been observed [33]. However, although dreams include clearly recognizable waking elements, they do not reproduce real-life events [16] as required by the consolidation models. This situation is, however, fully consistent with the resource management model. Consolidation models also have the problem that REM sleep deprivation appears to have relatively little effect on memory capabilities, and REM sleep can be substantially or completely suppressed (by various antidepressant drugs, or by bilateral damage to the pons) without apparent effect [35]. In agreement with these observations, in the resource management model deprivation of REM sleep would be expected to increase the resources required for memory support to some degree, but would not qualitatively interfere with memory creation.

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