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Computational Models of Hippocampal Function in Memory: Introduction to Special Issue

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This special issue of Hippocampus focuses on computational network models of hippocampal function, especially those that make substantive contact with data from behavioral studies of learning and memory.

The aim of this special issue is to provide the reader with a general understanding of the aims, accomplishments and limitations of computational approaches to understanding hippocampal function. Given the psychobiological perspective of this issue, we have not included those models that are strictly physiological, and concentrate solely on cellular or circuit-level phenomena. The main purpose of this special issue is to facilitate the comparison between different computational models, and to assist the non-mathematically inclined reader in understanding how and where these models can be used as tools for understanding and motivating empirical research, including physiological, anatomical, and behavioral studies. The articles included focus on describing the spirit and behavior of computational models, omitting most details on their exact mathematical underpinnings. A few mathematical equations are given where critical to this description.

Many of the models described in this issue evolved from the influential early model of Marr (1971) which, in turn, built upon Hebb's (1949) ideas on how associations are acquired between groups of cells to form functional assemblies in the brain. The basic network architecture described by Marr's theory is known as an autoassociator, a simple network architecture that learns to associate all components of an input pattern with all other components of the same pattern. Many of the models presented here -- including those by Rolls, Treves et al., Shen and McNaughton, and Hasselmo et al -- use Marr's framework for modeling episodic or event memories in the hippocampus, especially within hippocampal CA3 field which shares many of the basic connectivity requirements for an autoassociator. These models focus on the ability of the hippocampal region to perform fast, temporary storage, suggesting that this underlies the hippocampal region's role in episodic memory formation. This is consistent with the neuropsychological data showing that episodic memory impairments are the most obvious behavioral effects in human amnesia following hippocampal region damage.

Some of the hippocampal models presented in this issue have drawn on the details of hippocampal anatomy and physiology to argue that the hippocampus has the capacity for learning sequences of input patterns. These models are generally based on recurrent versions of Marr's autoassociative networks: given a partial input consisting of the present activation of the input nodes to a network, an autoassociative network can perform pattern completion and retrieve the predicted next state. Levy presents a model of hippocampal CA3 field as a sequence predictor and argues that this general sequence prediction paradigm can provide a computational unification of a variety of putative hippocampal-dependent functions including contextual sensitivity, configuration, and cognitive mapping. Granger et al. describes a model of the CA1 field incorporating an LTP learning rule in which the amount of potentiation depends on the order of arrival of afferent activity to a target neuron. They show that with this temporally-dependent LTP learning, the CA1 network model can learn to store brief simulated temporal sequences of inputs. Liaw and Berger also describe a model of hippocampal neurons in which they argue that the dynamic interplay of hippocampal synaptic mechanisms for facilitative and inhibitory processes results in an emergent "temporal chunking" mechanism for sequential pattern recognition.

Many theorists have noted that autoassociative memory systems seem ideal for implementing a spatial processor, in which the broad memory of a place could be evoked by any of several views of the area, even if some of the usual cues are missing. In fact, spatial memory is extremely hippocampal-dependent in rats (e.g., O'Keefe & Nadel, 1978), and many connectionist models of hippocampal-processing in spatial learning have been based on autoassociative models of the hippocampal region. Within this issue, the articles by Muller and Stead, Sharp et al., and Recce and Harris present alternative viewpoints regarding how the hippocampus may be involved in spatial navigation.

A pervasive idea in theories of hippocampal function is that the hippocampus is a fast, temporary storage system in which arbitrary patterns are stored. This aspect of hippocampal function is explored in this issue in the articles by McClelland and Goddard and by Murre. Both of these models assume that a relatively small temporary store in the hippocampus interacts with a relatively large neocortical system -- as suggested by Marr (1971) -- and use this to explain why patients exhibit (primarily) anterograde amnesia following hippocampal-region damage.

Another class of hippocampal models focus on hippocampal involvement in incrementally learned associative habits, such as classical conditioning or probabilistic pattern classification. Many recent qualitative theories and several computational models have focused on possible information processing roles for the hippocampal region which are most evident from studying complex training procedures in these incrementally-acquired associative learning tasks, such as classical and operant conditioning. The articles in this issue by Gluck and Myers and also Buhusi and Schmajuk both address the role of the hippocampal region in developing stimulus representations during associative learning.

In reviewing these psychobiological models of hippocampal function in learning and memory, three major themes have emerged. First, we see how computational models are often able to bind together data from multiple levels of analysis including cellular, physiological, anatomical, and behavioral studies. Some models are developed in a top-down fashion, beginning with detailed behavioral studies and then mapping functional processes to underlying biological substrates. Other models are developed in a more bottom-up fashion, beginning with biological details and then, via computer simulations, identifying emergent functional properties of these substrates (see Gluck & Granger, 1993, for further discussion of these distinctions in learning models).

A second theme that emerges is the importance of models as a tool to integrate data from both animal and human studies of hippocampal function in learning and memory. It seems clear that ultimately both animal and human studies of memory must converge more so that each body of literature and theory can better inform the other, hopefully leading to a more general and broadly applicable understanding of the hippocampal region in all species.

Finally, a third theme that emerges is the importance of relating current computational models to earlier traditions in memory research, especially the many earlier psychological models which capture important behavioral principles of memory. In drawing these connections between current models, and earlier qualitative theories in psychology and neurobiology, one can see the extent to which models represent cumulative progress.

To facilitate comparison and contrast among the many models presented in this issue, all of the articles generally follow a common format. Each article begins with an introduction that seeks to address several keys questions: 1. What is the goal of the model?; 2. What are the data to be explained? 3. How should the reader evaluate the model? The body of the paper consists of a synopsis of the current state of the author's computational model(s) of the hippocampal region and it's role in learning and memory. These reviews are designed to be accessible to most empirical researchers with no experience in formal modeling.

The final discussion section of each article is, in many ways, the primay contribution of these articles, and hence of this special issue. These discussion sections provide the basis upon which the different models can be evaluated, compared, and related to each other -- and to the agendas and interests of the experimental community. The discussion section of each paper includes four subheadings which address each of the following questions: 1. What do we know now that we didn't know before? 2. What did the model accomplish that couldn't have been accomplished by simpler, verbal-qualitative reasoning? 3. How does this model relate to others in this issue, and other non-computational theories that have been proposed? 4. What new experimental directions are suggested by this modeling, either (a) to test novel predictions or (b) to focus and direct future empirical studies?

All the models presented in this special issue represent preliminary attempts to incorporate both biological data and behavioral analysis within formal computationally-defined theories. As crude approximations to real biology at best, the value of these models will only become apparent if they lead to important new empirical studies which will inform and constrain future generations of models and theories.

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