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Review

Unfolding the cognitive map: The role of hippocampal and extra-hippocampal substrates based on a systems analysis of spatial processing

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ABSTRACT

What has been long absent in understanding the neural circuit that supports spatial processing is a thorough description and rigorous study of the distributed neural networks associated with spatial processing-both in the human as well as in rodents. Most of our understanding regarding the elucidation of a spatial neural circuit has been based on rodents and therefore the present manuscript will concentrate on that literature. There is a trend emerging in research to expand beyond the hippocampus for evaluating spatial memory, but the thrust of the research still focuses on the role of the hippocampus as essential and other neural substrates as performing subservient roles to support hippocampus-dependent spatial processing. This review will describe spatial memory in terms of a system model incorporating partially overlapping and interacting event-based, knowledge-based and rule-based memory systems that are composed of different component processes or attributes associated with spatial processing which are mapped onto the corresponding neural substrates and larger networks. In particular, the interactions among brain systems that process spatial information will be emphasized. We propose that these interactions among brain regions are essential for spatial memory.

1. Introduction

In this paper we will present a neural circuit analysis of memory representation of spatial memory within the context of the attribute model of memory. We will concentrate primarily on research carried out with rodents. We also will propose and describe a research methodology that is highly applicable for studying distributed systems within the rodent brain. Memory for spatial information is fairly complicated and involves a wide and diverse neural network in addition to the medial temporal lobe and hippocampus. Kesner (1998), Kesner and DiMattia (1987), Kesner, Evans, and Hunt (1986), Kesner and Ragozzino (2003) has proposed a tripartite attribute based theoretical model of memory to account for this complexity in modeling brain function. This tripartite attribute specificity model is organized into event-based, knowledge-based, and rule-based memory systems. Each of these individual memory systems is comprised of overlapping attributes or forms of memory. These process-oriented attributes can be easily mapped onto neural networks and interconnected circuits. For more details of the model see Hunsaker (2013), Kesner (1998, 2002, 2013c, 2016). The high level of anatomical inter-connectivity and functional interactions proposed in these models have been diagrammed in Fig. 1 and will be expanded upon in the present review (*cf.*, Figs. 2 and 3).

At a psychological level, the event-based memory system subserves transient spatial representations of incoming data concerning present inputs, with an emphasis upon data and events that are personal or egocentric and occur within specific contexts. The emphasis of the event-based memory system is on the processing of current information that is novel. The event-based memory system is emphasized during the initial phases of learning, and will continue to be greatly important even after learning, so long as behavioral situations require unique or novel trial information need to be processed or remembered. This system is somewhat comparable to episodic memory and some aspects of declarative memory (Squire, 1992, 2004; Tulving, 1994).

The knowledge-based memory system subserves more long lasting, permanent representations of already encoded spatial information in long-term memory. Knowledge-based memory can be conceptualized of as general spatial knowledge. As such, the knowledge-based memory system is of greater importance once a task has been learned, so long as the behavioral situation is relatively invariant and familiar. Within the knowledge-based memory system, the organization of the spatial attribute is organized as a set of interacting cognitive maps and their interactions that are unique for each memory (Hunsaker, 2013; Kesner, 2013).

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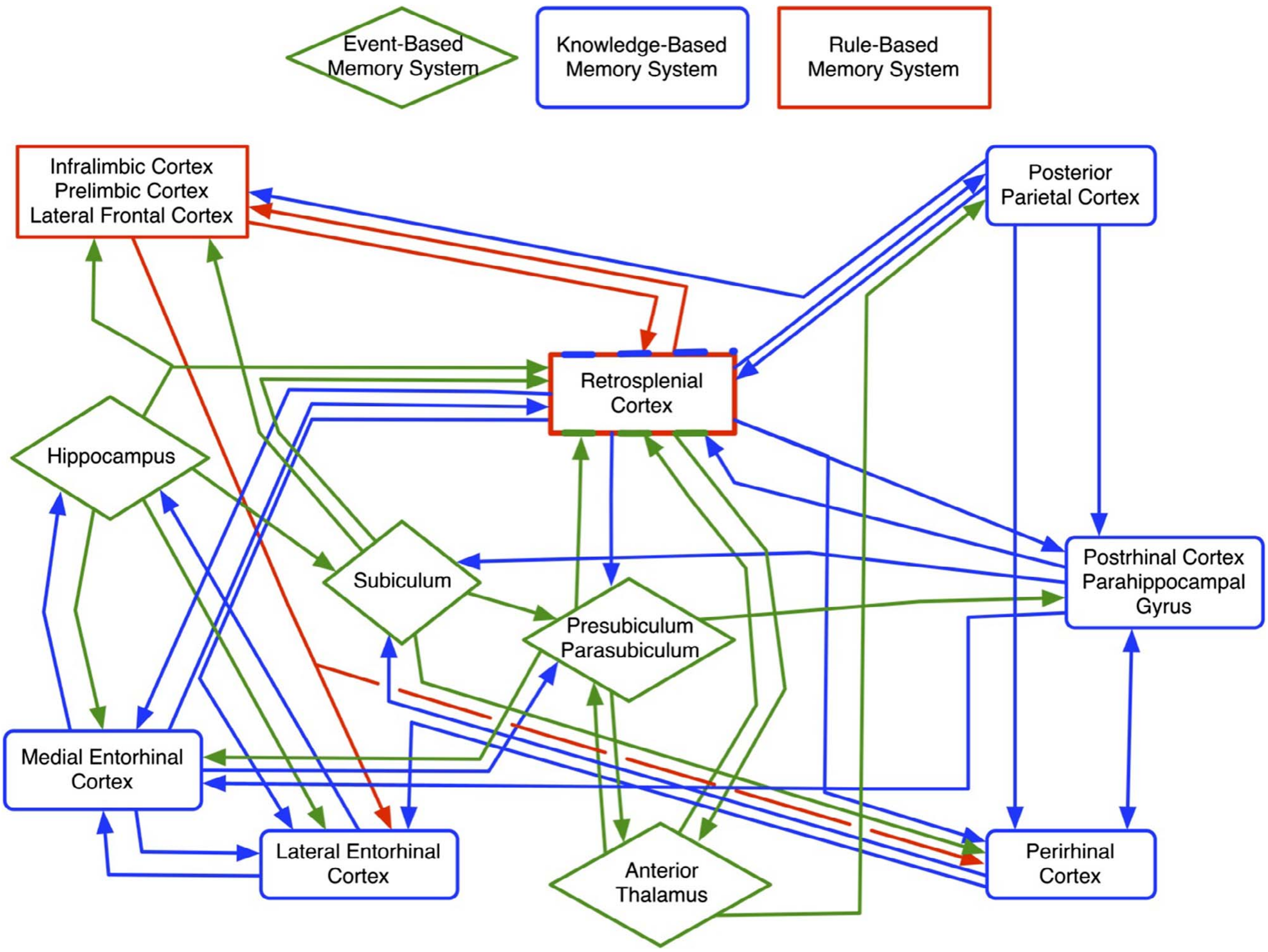

Fig. 1. Neural networks involved in processing the spatial attribute within the event-based memory system, the knowledge-based memory system, and rule-based memory system. Particular attention should be paid to the interactive nature of these neural networks for spatial processing. These interactions are possible given the rich anatomical connectivity among these brain regions, as shown in later figures.

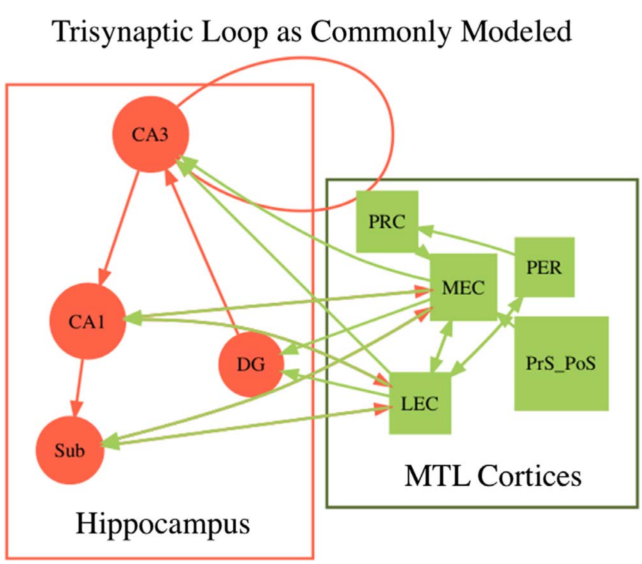

Fig. 2. Diagram of the simplified trisynaptic loop often used in simulations of hippocampus function. This is a convenient simplification for hypothesis testing, but the reality of hippocampus wiring is much more complex. We propose this over-simplified model should be replaced by models accounting for the field's increased knowledge of anatomic and molecular connectivity given the improvement in computational resources since the inception of this simplified model by "Simple memory: A theory for archicortex (1971).

The rule-based memory system integrates spatial information from both the event-based and knowledge-based memory systems and applies rules and strategies that are necessary to guide subsequent action. In most situations, one would expect that all three systems with a varying proportion of involvement to provide behaviorally relevant contributions to spatial learning and memory processing (Kesner, 1998, 2013c; Kesner & Ragozzino, 2003).

Importantly, these event-based, knowledge-based, and rule-based memory systems are composed of the same attributes of memory. A spatial attribute within this attribute framework includes mnemonic representations of places or relationships among places. The spatial attribute is exemplified by the ability to encode and retrieve spatial maps and to localize stimuli in external space. Memory representations of the spatial attribute are further subdivided into specific features including allocentric spatial distance, egocentric spatial distance, allocentric direction, egocentric direction, metric and topological space, spatial location, and spatial context. In addition, there are specific spatial features associated with spatial navigation such as head direction and path integration (Hunsaker, 2013; Kesner, 1998).

Within each system, information related to the spatial attribute is differentially processed based on the operational characteristics of each memory system. For the event-based memory system, specific processes involve (a) selective filtering or attenuation of interference of temporary memory representations of new information and is labeled pattern separation, (b) encoding of new information, (c) short-term and intermediate-term memory for new information, (c) the establishment of arbitrary associations, (d) consolidation or elaborative rehearsal of