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Mnemonic functions of the hippocampus: A comparison between animals and humans

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Abstract

This review summarizes a series of experiments aimed at answering the question whether the hippocampus in rats and humans performs parallel functions focusing on studies that assess spatial and temporal pattern separation, sequential learning, spatial and temporal pattern association, spatial and temporal pattern completion, and short-term and intermediate-term memory. It is recognized that a comparison of the functions of the rat hippocampus with human hippocampus is difficult, because of differences in methodology, differences in complexity of life experiences, and differences in the degree of hippocampal damage as well as damage to interconnected brain regions. Yet, in general the data support the idea that with respect to spatial and temporal pattern separation, sequential learning, spatial and temporal pattern associations, spatial and temporal pattern completion, and short-term and intermediate-term memory, similar functions are observed in rats and humans with hippocampal damage using analogous tasks. These data provide support for evolutionary continuity in cognitive function assigned to the hippocampus of rats and humans.

Keywords: Pattern separation; Sequential learning; Pattern association; Pattern completion; Short- and intermediate-term memory

1. Introduction

Memory is extremely complex in terms of the kind of information that is represented in the brain, the processes associated with it, and its distribution across a variety of neural systems. For example memory for skills, habits, priming, and simple classical conditioning involve a variety of brain regions including the striatum, amygdala, frontal lobes, and cerebellum. For many years the hippocampus has been thought to play a very important role in processing new information leading to learning and memory in both animals and humans. The anatomy of the hippocampus is complex but understood better than many other brain regions. For excellent reviews of hippocampal anatomy in the rat and humans (see Amaral and Witter, 1995; Amaral and Insausti, 1990). This paper will primarily focus on the mnemonic functions of the hippocampus in animals and humans.

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Although there is some agreement regarding the mnemonic functions of the hippocampus in terms of the nature of memory representation and the processes that support these memory representations, there are some important differences between theories that remain the subject of discussion. These differences regarding hippocampal function are directly related to the nature of the memory representation, the duration of memory representations (i.e. short, versus intermediate, versus long-term), and some functions of mnemonic processing such as pattern separation, pattern association, and pattern completion. Pattern separation can be defined as the ability of the hippocampus to encode and separate events in space and time, pattern association is the ability to form arbitrary associations between events and items, and pattern completion is a mechanism that can generate complete retrieval of well-established information based on partial or incomplete inputs. For example, Squire (1994) has suggested that the hippocampus is very important for encoding, consolidation and episodic memory (intermediate, but not short or long-term memory) processes for all types of information including processing of temporal, spatial, sensory perceptual (odors, visual objects, and sounds), response, reward value, and linguistic information.

Olton et al. (1979) have proposed that the hippocampus is involved in encoding, consolidation and episodic memory (short and intermediate, but not long-term memory) processes for all types of information. Eichenbaum (2002) has suggested that the hippocampus supports encoding, consolidation and episodic memory (short and intermediate, but not long-term memory) processes and retrieval based on flexibility for all types of relational information including association between arbitrary stimuli. O'Keefe and Nadel (1978) propose that the hippocampus mediates encoding, consolidation and episodic memory (short, intermediate and long-term memory) for primarily spatial information. Rolls (1996) has suggested that the hippocampus, based on subregional specificity, supports encoding, consolidation and episodic memory (short and intermediate, but not long-term memory), pattern separation, pattern association as well as retrieval often based on pattern completion for all types of information. Kesner (1998a) has suggested that the hippocampus, based on subregional specificity, supports encoding, consolidation and episodic memory (short and intermediate, but not long-term memory), pattern separation, pattern association and retrieval often based on pattern completion for spatial and temporal information for both animals and humans, and linguistic information for humans. Short-term and intermediate-term memory, pattern separation, pattern association, and pattern completion processes can be thought of as intrinsic functions of the hippocampus. However, intermediate and long-term memory, consolidation and some forms of retrieval may be extrinsic to the hippocampus, as they require extensive cooperation between the hippocampus and other interrelated brain regions. Notice that intermediate-term memory can operate as both an intrinsic and extrinsic function of the hippocampus.

Thus, the major differences that emerge regarding hippocampus function are directly related to the nature of the memory representation for all types of information (Eichenbaum, 2002; Olton et al., 1979; Rolls, 1996; Squire, 1994), versus only spatial (O'Keefe and Nadel, 1978), and only spatial, temporal and linguistic information (Kesner, 1998a). In terms of processing of information, there are differences regarding the duration of memory representations with some suggesting that the hippocampus is critical for processing information within both short-term and intermediate-term memory, but not long-term memory (Eichenbaum, 1999, 2002; Kesner, 1998a; Olton et al., 1979; Rolls, 1996). In contrast, Squire (1994) suggests that the hippocampus is important only for intermediate-term memory, whereas O'Keefe and Nadel (1978) suggest that the hippocampus is involved in short-, intermediate-, and long-term memory. Also, there are differences concerning the operation of functions other than encoding, retrieval and consolidation such as pattern separation, pattern association, and pattern completion. Only Rolls (1996) and Kesner (1998a) acknowledge the importance of these additional functions of the hippocampus.

The purpose of the present review is to determine that the hippocampus in rats and humans performs parallel functions, focusing on intrinsic information processing exemplified by pattern separation, association and completion, sequential learning, short-term memory and intermediate-term memory. We recognize that a comparison of the function of rat hippocampus with human hippocampus can be quite difficult. Campbell and Hodos (1970) suggest that one can evaluate homologies between rats and humans based extensively on behavioral changes following brain lesions. It should, therefore, be possible to determine whether homologies exist between rats and humans based on changes associated with spatial and temporal pattern separation, sequential learning, spatial and temporal pattern association, spatial and temporal pattern completion, and short-term and intermediate-term memory processes following damage of the hippocampus in rats and humans.

2. Pattern separation

Previous research indicates that the hippocampus received inputs from all sensory modalities, suggesting that one possible function of the hippocampus is to use sensory markers to demarcate a spatial location, allowing the hippocampus to more efficiently represent spatial information. Thus, one function of the hippocampus may be to encode and separate events in space resulting in spatial pattern separation. Spatial pattern separation would ensure that new highly processed sensory information is organized within the hippocampus, which in turn enhances the possibility of remembering and temporarily storing one place as separate from another place. The separation of events may occur via pattern separation of spatial information, so that spatial locations are separated from each other and spatial interference is reduced. It should be noted that the idea that the hippocampus supports context as well as spatial arrangement of objects (Jenkins et al., 2004; Lee and Kesner, 2004) is consistent with the need to separate objects and/or other cues to achieve optimal spatial representations. Pattern separation is akin to the idea that the hippocampus is involved in orthogonalization of sensory input information, in representational differentiation, and indirectly in the utilization of relationships.

2.1. Spatial pattern separation

2.1.1. Experiments in rats

To investigate the role of the hippocampus in the separation of spatial events based on the overlapping similarity of distal cues, we developed a unique paradigm in which rats were required to remember a spatial location dependent on spatial cues. In a pattern separation task rats are required to remember a spatial location dependent upon the distance between a study phase object and an identical object used as a foil in a different location (Gilbert et al., 1998). During the study phase, an object that covers a baited food well is randomly positioned in one of 15 possible spatial locations on a cheese board. Rats exit a start box and displace the object in order to receive a food award and then return to the start box. On the ensuing test phase rats are allowed to choose between two objects, which are identical to the object in study phase. One object is baited and positioned in the previous study phase location (correct choice), the other (foil) is unbaited and placed in a different location (incorrect choice). Five distances (minimum = 15 cm, maximum = 105 cm), randomly