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The role of the hippocampus in the retrieval of a spatial location

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Abstract

Based on computational models of the hippocampus, it has been suggested that a possible mechanism for memory retrieval is pattern completion, wherein an autoassociative network recalls previous patterns of activity given noisy or degraded cues. However, there are few behavioral data examining pattern completion per se in the hippocampus. Here, we present a study in which rats were tested on a spatial location retrieval paradigm, each trial of which consisted of a sample and choice phase. During the sample phase, rats were trained to displace an object in one of 15 possible locations to retrieve a food reward and return to the start-box on a cheeseboard maze. The object was then removed and the same location was re-baited for the choice phase. The rats' accuracy in returning to the correct location was recorded. On test trials, visual extramaze cues, vestibular cues, or both were manipulated to assess pattern completion in normal rats. Subjects were then randomly assigned to receive a cortical control, a sham, or a dorsal and ventral hippocampal lesion and were retested on the task. Control and unoperated rats were able to perform the task when visual extramaze or vestibular cues were reliable, but not when they were manipulated. Rats with hippocampal lesions were impaired in the baseline condition, as well as during all manipulations. These results support the hypothesis that the hippocampus supports the retrieval of a spatial location, possibly through a process of pattern completion.
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Keywords: Memory; Rat; Hippocampus; Pattern completion

1. Introduction

Among other things, the hippocampus plays a central role in spatial learning and memory (Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999; Morris, Garrud, Rawlins, & O'Keefe, 1982; O'Keefe & Nadel, 1978). One mechanism through which the hippocampus aids in memory retrieval as proposed by computational models is pattern completion (Marr, 1971; McNaughton & Morris, 1987; O'Reilly & McClelland, 1994; Recce & Harris, 1996; Willshaw & Buckingham, 1990); the ability to retrieve a stored memory trace based on an incomplete or degraded set of sensory cues. Based on neural connectivity, Marr (1971) originally proposed a dual memory system made up of cortical and hippocampal components. Marr suggested that the hippocampus contains an autoassociative network, that is, a network of interconnected neurons in which a simple representation of an input is formed. Subsequent models of hippocampal function (Kesner & Rolls, 2001; Rolls, 1989, 1996; Stringer, Rolls, Trappenberg, & deAraujo, 2002; Stringer, Trappenberg, Rolls, & deAraujo, 2002) have also proposed that the hippocampus is able to quickly store memories using an autoassociative network. According to Rolls (1996), "the hippocampus contains one stage, the CA3 stage, which acts as an autoassociation memory." As evidence for the role of CA3 in pattern completion, Rolls and colleagues (Robertson, Rolls, Georges Francois, & Panzeri, 1998; Rolls, Robertson, & Georg-

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es-Francois, 1997) report that some cells in CA3 respond when a monkey's view of a particular part of space is briefly obscured by a curtain or darkness. This pattern of firing may reflect a completion of the scene in the absence of the visual input.

Few studies have directly examined the role of the hippocampus in pattern completion. Perhaps the most direct assessment of the hippocampus's role in pattern completion was made by Nakazawa and colleagues using knockout mice which had the NMDA receptor gene ablated in CA3 (Nakazawa et al., 2002). Knockout mice were found to be impaired relative to controls on probe trials of a spatial memory task when only a subset of extramaze spatial cues which were present at training was presented. Indeed in a subsequent lesion study, rats with CA3 and dentate gyrus lesions, but not CA1 or sham control lesions, were impaired when a subset of visual extramaze cues were present during the test phase of a spatial pattern completion task (Gold & Kesner, 2003). While it is apparent from these studies that animals use visual stimuli when performing a spatial pattern completion task, it is unclear whether egocentric information is also used. According to several models of hippocampal function (Knierim, Kudrimoti, & McNaughton, 1998; Rolls, 1999), allocentric (environment-centered visual) and egocentric (idiothetic or vestibular) information interact in the formation and maintenance of spatial memory traces.

The present study proposes to further test the predictions of the computational models using a behavioral paradigm. Specifically, we were interested in first determining if normal rats are able to retrieve a spatial location given degraded allocentric and/or egocentric cues, and second, to what extent the hippocampus is involved in the retrieval process.

2. Method

2.1. Subjects

Subjects were 13 male, Long–Evans rats, each weighing ~350 g at the beginning of testing. Each rat was initially food deprived to 80% of its free-feeding weight and allowed access to water ad libitum. Rats were housed individually in standard rodent cages and were maintained on a 12 h light/dark cycle. All testing was performed during the light phase of the cycle.

2.2. Apparatus

The test apparatus was a dry-land version of the Morris water maze, or "cheeseboard" maze apparatus. The surface of the apparatus stood 65 cm above the floor, was painted white and was 119 cm in diameter and 3.5 cm in thickness. One hundred seventy-seven food wells, 2.5 cm in diameter and 1.5 cm in depth, were drilled into the surface of the maze in evenly space parallel rows and columns 2 cm apart. The bottom of each food well had a small compartment separated by wire mesh containing a piece of food reward (Froot Loops cereal) to prevent rats from using the olfactory cues to locate the correct location on the maze. The maze was kept in a well-lit room with no windows, one door, a chair, a shelf, and three pictures of various sizes on three of the walls. During testing, each animal was first placed in a start-box, which is 24 cm long, 15 cm wide and 17 cm high and was placed on the maze surface centered perpendicular to the rows of food wells. The box was equipped with a removable top and a guillotine door, which may be raised and lowered manually by the experimenter. A clear Plexiglas partition (7 cm deep and 8 cm tall) with fifteen 7 cm openings to permit the animal access to each well individually was placed on the centermost row of food wells perpendicular to the start box. The partition forced the rat to enter each individual opening in order to explore each food well. A black nylon curtain was suspended above the maze and could be lowered around the maze by a network of ropes and pulleys so as to block visual access to extramaze cues during the visual manipulation.

2.3. Preoperative testing

Naïve rats were initially introduced to the apparatus and shaped to displace a neutral object to receive a food reward. Once this was accomplished, training on the task began. The general procedure for the task was as follows: Each trial consisted of a sample and choice phase. During the sample phase of the task, an object was placed over 1 of 15 food wells along the center most row of wells on the maze, perpendicular to the start-box. The 12 target locations for each day of testing were pseudorandomly chosen, such that each of the 15 possible locations had an equal likelihood of being chosen for any given trial. Target locations were not repeated within a single day of testing. The target object was a small black block, 2.5 cm by 2.5 cm by 4 cm. The sample phase began with the opening of the start-box door, the animal then exited the box and displaced the object in order to receive a reward. The animal then returned to the start-box and the door was again closed. The same food well was quickly re-baited; however in this case, no object was placed over the food well. The delay between sample and choice phases was approximately 5 seconds. For the choice phase, the door was re-opened and the animal was allowed to explore the wells until the food reward was located. The first location the animal searched for the food reward (i.e., the first partition entered) on the choice phase was recorded. Accuracy was measured in terms of difference in degrees between the target and actual choice. Degree differences between

target locations were determined by measuring the degrees between the center of each partition opening relative to the center of the door of the start-box. Throughout testing, animals were run for 12 consecutive trials per day and then returned to their home cage. During preoperative training, each rat had access to all visual extramaze cues. Each animal was tested until it reached a criterion of searching within 18° of visual angle of the target location, averaged across 48 trials. Prior to reaching criterion, a corrective procedure was implemented whereby animals were picked up off the maze and immediately returned to the start-box without receiving a reward after an incorrect choice. Since we specifically were not manipulating local visual or olfactory information on the maze, the maze was wiped down at the end of each testing day with a cleaning solution.

Once the animals' performance reached criterion, the cues available to complete the task were manipulated to assess the animals' ability to complete the spatial pattern when either extramaze visual or internal vestibular information or both were unreliable. For the preoperative test block, animals were presented with 12 baseline trials as described above, 12 trials in which access to extramaze visual cues was restricted only on the choice phases by lowering a black curtain around the maze, and 12 trials in which vestibular information was manipulated by slowly rotating the start box on the maze between the sample and choice phases. The trials were pseudorandomly mixed, with 4 of each trial per day, for 3 test days. Following the initial test block, rats received an additional block of 12 more baseline trials randomly intermixed with 12 trials when both visual and vestibular information was manipulated (six of each trial pseudorandomly intermixed for 2 test days). The test manipulations forced the rat to locate the food reward in the absence of either distal visual cues, internal vestibular cues, or a combination of both. These manipulations were administered randomly, thus preventing the rat from predicting which cues were manipulated on any choice phase. The rat therefore was forced to attend to all available cues on the sample phase in order to have a reliable representation of the target location such that it would be able to retrieve the food reward on the choice phase. Once the preoperative testing block was complete, rats were scheduled for surgery.

2.4. Surgery

Each animal was assigned to receive either an electrolytic lesion of the dorsal hippocampus, dorsal and ventral hippocampus (HIP), or was assigned to a control group (CON) with either a cortical control or a sham lesion. Prior to surgery, each rat was given atropine sulfate (0.2 mg/kg, i.p.) and anesthetized with sodium pentobarbital (Nembutal; 60 mg/kg, i.p.). Each animal was then placed in a stereotaxic instrument, and an incision was made in the skin covering the skull. The bone overlying the lesion site was then removed with a small dental burr. Electrolytic lesions of the hippocampus were generated by passing a 1.2-mA anodal current for 10 s through a stainless steel electrode (0.35 mm in diameter) insulated with Epoxylite except for ~0.50–0.75 mm at the tip of the electrode. The coordinates for the dorsal hippocampal lesion were 3.5 mm posterior to bregma, 3.4, 2.2, and 1.0 mm lateral to midline, and 2.8 mm ventral from skull. The coordinates for the ventral hippocampal lesion were 4.6 mm posterior to bregma, 5.2 mm lateral from midline, and 8.1 and 5.6 mm ventral from skull. Cortical control lesions were at the same coordinates, but the electrode was lowered 1.0mm ventral from the skull. Sham lesions were made by lowering the electrode at the same coordinates for the dorsal hippocampus, but no current was passed through the electrode.

2.5. Postoperative testing

After a week recovery period, each rat was again tested as described for the preoperative testing with 12 trials each of the baseline, vestibular, visual, and combination manipulations.

2.6. Histology

At the conclusion of all testing, each animal was deeply anesthetized with an intraperitoneal injection of 1.5 ml sodium pentobarbital (60 mg/kg), and perfused intracardially followed by a 10% formalin solution. The brain was removed from the skull and stored in a 10% formalin/30% sucrose solution. Each brain was frozen and cut at 24 μm sections starting at bregma and extending through the posterior region of the hippocampus. Every third section was mounted on a glass slide, stained with cresyl violet, and examined for histological verification of the lesion placement.

3. Results

Sham and cortical control lesions showed no behavioral or hippocampal anatomical differences and were therefore combined into a single lesion group ($n = 7$). A repeated measures two-way analysis of variance revealed no main effect for lesion between the dorsal ($n = 3$) and dorsal plus ventral hippocampal ($n = 3$) lesion groups ($F(1, 4) = 3.756$; $p = .125$) and no manipulation by lesion interaction for the POST block ($F(1,4) = 0.535$; $p = .667$). Since the two groups' performance did not differ significantly, they were therefore combined into one group for the purpose of data analysis. Fig. 1A is a representation of the largest and smallest hippocampal lesions. Damage was primarily confined to

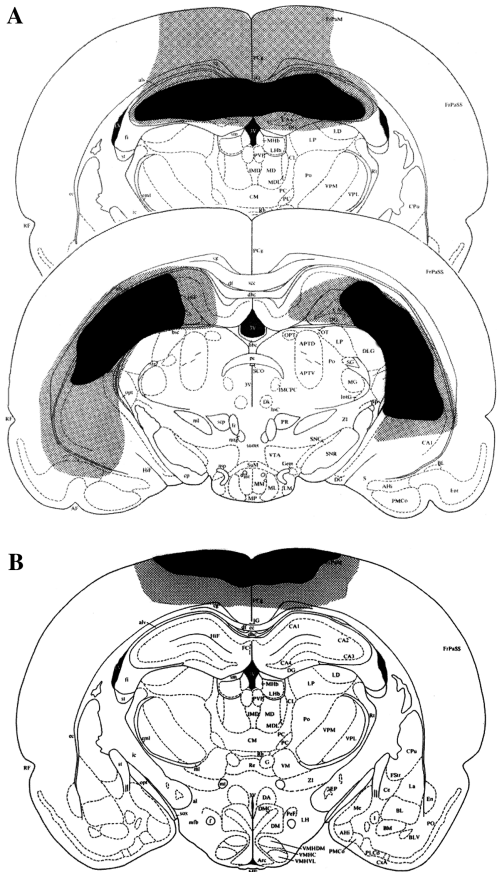

Fig. 1. A schematic representation of the largest (stippled) and smallest (solid) hippocampal (A) and control cortical (B) lesions. Slice locations are Bregma −3.3 mm (A top & B) and Bregma −4.8 mm (A bottom). See Paxinos and Watson (1986).

the hippocampus, but cortical damage dorsal to the hippocampus was observed in a subset of rats. Fig. 1B is a representation of an example cortical control lesion. Damage was located primarily in cortex dorsal to the dorsal hippocampus.

3.1. Behavioral performance

Normal, unoperated rats were capable of retrieving a spatial location during the baseline manipulation, however, hippocampal lesioned rats were impaired even at baseline. Fig. 2A shows the performance of CON and HIP groups for the PRE and POST blocks on the baseline manipulation. Chance performance was calculated by taking the average of the possible angular errors associated with each choice location, and is indicated by the dashed line in Fig. 2. For the PRE block, both groups performed significantly better than chance [($t(6) = -28.606$; $p < .001$) and ($t(5) = -10.924$; $p < .001$) for the CON and HIP groups, respectively], and the CON group was again better than chance in the POST block ($t(6) = -19.183$; $p < .001$). The HIP group, however, fell to near chance performance in the baseline condition ($t(5) = -2.507$; $p = .054$). A two (CON vs. HIP) by two (PRE vs. POST) ANOVA revealed a significant main effect of block ($F(1) = 21.016$; $p < .001$), a main effect of lesion ($F(1) = 7.883$; $p < .05$) and a significant block by lesion interaction ($F(1) = 47.301$; $p < .001$). Thus, normal and unoperated rats are capable of retrieving a spatial location given degraded cues, but rats with hippocampal lesions are not, indicating that spatial pattern completion requires the hippocampus.

Normal, unoperated rats were also able to retrieve a spatial location when vestibular cues were also manipulated, but hippocampal lesioned rats were not. When distal maze cues were manipulated, neither group was significantly better than chance. Fig. 2B shows the performance of CON and HIP groups for the PRE and POST blocks on the vestibular manipulation. In this manipulation, both groups' PRE performance was significantly better than chance, ($t(6) = -7.049$; $p < .001$) and ($t(5) = -3.395$; $p < .05$) for the CON and HIP groups, respectively. For the POST block, the CON group performed better than chance, ($t(6) = -2.87$; $p < .05$), however the HIP group was at chance performance. A 2×2 ANOVA revealed a main effect of lesion ($F(1) = 12.298$; $p < .01$), however, in this case the block by lesion interaction was not significant ($F(1) = 2.596$; $p = .135$). Fig. 2C shows the performance of CON and HIP groups for the PRE and POST blocks on the visual manipulation. For this manipulation, even the CON group's performance was not significantly better than chance for the PRE ($t(6) = -.913$; $p = .396$) or the POST blocks ($t(6) = -2.11$; $p = .079$), indicating that normal animals relied heavily on visual extramaze cues when solving the spatial pattern completion task. For the visual manipulation, the block by lesion interaction was not significant, ($F(1) = 4.062$; $p = .069$). Fig. 2D shows the performance of CON and HIP groups for the PRE and POST blocks on the combination of the vestibular and visual manipulation. When both vestibular and visual cues were unreliable, both groups' performance was at or worse than chance. For this manipulation, the 2×2 ANOVA revealed a main effect of lesion approaching significance ($F(1) = 4.653$; $p = .054$), however, there was no significant block by lesion interaction, ($F(1) = .437$; $p = .522$). The results of the combination manipulation indicate that without reliable vestibular or visual cues, even intact animals were unable to retrieve a spatial location for a food reward.

4. Discussion

The above results indicate that normal rats are able to retrieve a spatial location given partial or degraded cues, as in the case of the vestibular manipulation. However, if visual cues used to encode a location are manipulated, normal rats do not have enough input on which

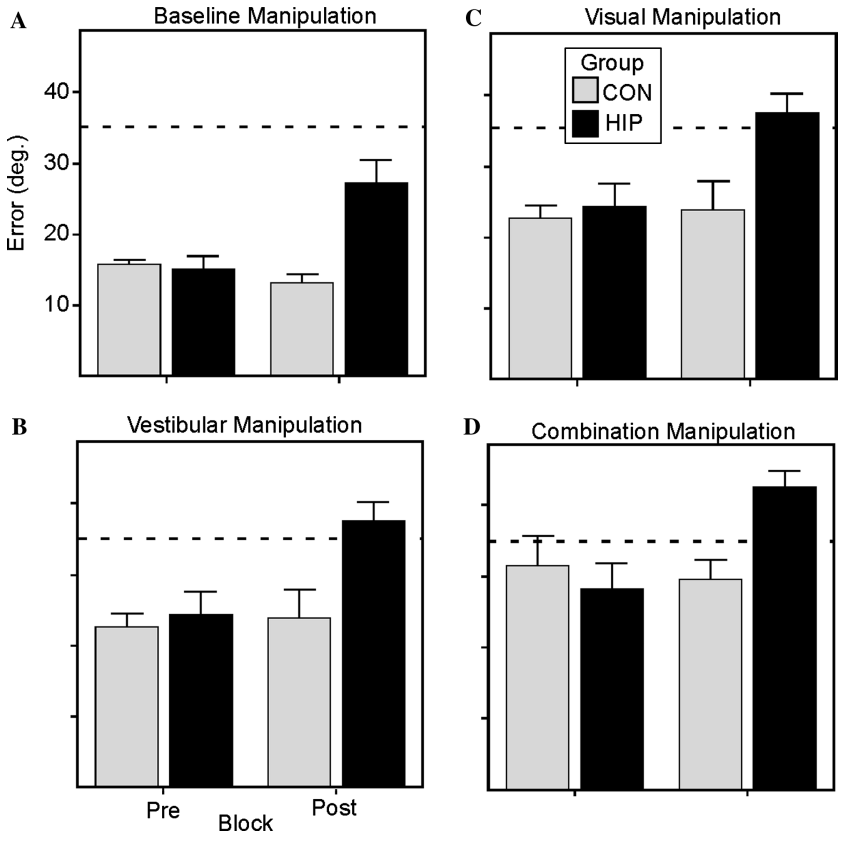

Fig. 2. Performance of CON and HIP groups in the PRE and POST testing blocks for the baseline (A), vestibular (B), visual (C), and combination (D) manipulations. Chance performance is indicated by the dashed line.

to complete. These results are consistent with the observation that in normal rats place fields recorded in CA1 region of the hippocampus became unstable when all significant distance cues were removed (O'Keefe & Conway, 1978). Hippocampus lesioned rats are impaired at baseline as well as when visual/vestibular cues are manipulated indicating that the hippocampus is necessary for the retrieval of spatial locations.

Few studies have examined pattern completion directly. Rudy and O'Reilly (1999) examined the role of pattern completion in contextual fear conditioning, a process known to be hippocampal dependent (Phillips & LeDoux, 1992, 1994). Rudy and O'Reilly (1999) used a pattern completion paradigm to assess contextual encoding properties of normal animals. They found that normal animals consistently displayed freezing behavior when presented with a subset of environmental cues, which were present during contextual fear training. Eichenbaum and colleagues have also proposed that the hippocampus is necessary for "flexible memory expression" (Dusek & Eichenbaum, 1997; Eichenbaum et al., 1999) which can be interpreted as a form of pattern completion (Kesner, Gilbert, & Barua, 2002; Kesner, Gilbert, & Wallenstein, 2000).

The results of the current study can be contrasted with those recently reported by Alyan, Jander, and Best (2000), who found that hippocampectomized rats are able to recognize a place using a constellation of landmarks on a pattern completion type task using a reference memory paradigm. However, in this study the rat did not have to remember a different target location for each trial, as in the current study. Therefore, hippocampal dependent pattern completion may be for working memory representations such as in the present task where a location must be remembered between phases of each single trial, but not needed after that. Similar impairments in retrieval due to hippocampal damage have already been reported. Rats with hippocampal damage have been shown to have deficits in conditional retrieval processes (Hirsh, 1980) where retrieval must extract one piece of acquired information over another, similar piece. Hippocampus damage also results in impairments in ability to generalize between stimuli in a classical conditioning paradigm (Freeman & Kramarcy, 1974).

These deficits can be explained in terms of failure to complete a spatial pattern based on both egocentric (vestibular) and allocentric (spatial) information. The hippocampus receives input from several sensory modalities, which it can use to assist an animal in navigating through an environment. Salient cues include both allocentric and egocentric cues. Both types of information can be used equally effectively to solve spatial navigation tasks (Mog-

haddam & Bures, 1996). One important source of egocentric information is the vestibular system (Berthoz & Israël, 1996). It has been shown that place cells in the hippocampus respond to either vestibular input (Smith, 1997), or visual landmark information, or both (Knierim, Kudrimoti, Skaggs, & McNaughton, 1996; Sharp & Blair, 1995). Rolls and colleagues' (Rolls, Stringer, & Trappenberg, 2002) model also predicts that animals are able to update their representation of where they are in space using ideothetic information in the absence of visual cues. The autoassociative network found in the hippocampus may be able to recall stored spatial patterns with either vestibular or spatial input. Jeffery and O'Keefe (1999) have demonstrated that hippocampal place cells initially respond based on visual information, but ideothetic cues gain preference when visual information becomes unreliable. This is consistent with the results of the spatial manipulation in the current study. High error rates on trials when spatial cues were manipulated indicate that rats rely preferentially on spatial cues rather than vestibular or other cues. Interestingly, this pattern of results holds for control as well as hippocampal lesioned animals.

The current study indicates that controls are able to form a short-term spatial representation sufficient for pattern completion when presented with partial cues. Also, complete lesions of the hippocampus may decrease efficiency in pattern completion. Computational models suggest that subregions of the hippocampus, specifically CA3, support pattern completion (Kesner & Rolls, 2001; Marr, 1971; Rolls, 1989, 1996; Shapiro & Olton, 1994). The results of a recent study by Nakazawa and colleagues (Nakazawa et al., 2002) suggest that CA3 lesioned animals may be impaired relative to controls when presented with a subset of visual cues. However, when no visual cues are presented, CA3 and control groups are equally impaired. Further research into the mechanisms of pattern completion would include selectively examining the role played by subregions of the hippocampus in pattern completion in the presence of a subset of visual cues present at training.

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