

# Disambiguation of Similar Object-Place Paired Associations and the Roles of the Brain Structures in the Medial Temporal Lobe

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## ABSTRACT

Amnesic patients who have damage in the hippocampus and in associated areas in the medial temporal lobe suffer from remembering specific events that may or may not share similar objects and locations. Computational models, behavioral studies, and physiological findings all suggest that neural circuits in the hippocampus are suitable for representing seemingly similar events as distinctively different individual event memories. This article offers a selective review on this particular function of the hippocampus and its associated areas such as the perirhinal cortex, mostly centering upon lesion studies and physiological studies using animals. We also present recent experimental results showing that the dentate gyrus subfield of the hippocampus and perirhinal cortex are particularly important for discriminating similar paired associates between same objects and different locations, or *vice versa*.

**Key words:** hippocampus, perirhinal cortex, event memory, pattern separation

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## INTRODUCTION

Many studies using animals and humans suggest that the hippocampus is critical for remembering events (Hasselmo, 2005; Chadwick et al., 2010; Chadwick, 2010). Throughout this article, we define an "event" as a particular combination of individual items in a specific location in space and possible actions of an animal towards the items. Patients with hippocampal damage typically exhibit deficits in remembering discrete events composed of different places and associated items. Remembering a particular event often requires associating different

locations and objects, and several theoretical models suggest that such object-place association is likely to be represented in the hippocampus. Furthermore, maintaining distinct event memories also requires disambiguating similar events because different events may share common elements such as overlapping objects and/or same/similar places. Literature suggests that the hippocampus is essential in disambiguating similar places (Gaffan, 1994; Eacott et al., 2004; Kesner et al., 2008) and this implies that it may be also critical for the orthogonalization of neural representations for similar paired-associates between objects and places.

Brief overview of anatomical connections within the hippocampus as well as between the hippocampus and its associated regions will be provided here to help readers. The hippocampus receives most of its inputs from the entorhinal cortex (Bur-

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well et al., 1995). The entorhinal cortex is divided into the lateral entorhinal cortex (LEC) and the medial entorhinal cortex (MEC). The MEC receives most of its inputs from the POR and the inputs to the LEC mostly stem from the perirhinal cortex (PER) (Burwell et al., 1995). Anatomical literature indicates that the PER receives information that is qualitatively different from the information fed to the postrhinal cortex (POR). The POR receives its inputs from visual association and visuospatial cortex and this input has visuo-spatial characteristics in terms of quality of information and the postrhinal cortical cells have spatial selectivity (Burwell and Hafeman, 2003). On the other hand, the PER neurons receive inputs from the ventral visual sensory areas and it is known to respond to visual, somatosensory, auditory or a combination of sensory stimuli (Chadwick et al., 2010). Especially in physiological studies in the rat, the PER has been identified to exhibit response-selectivity to odor and visual stimuli (Young, 1995; Zhu et al., 1995; Young et al., 1997). Gaffan and colleagues provided evidence that PER lesion in monkeys produce impairment in discriminating large numbers of visual stimuli. Based on this finding, the authors argued that the PER participates in sensory functions, including object identification (Eacott et al., 1994) and Burwell also found that cells in the PER fire in correlation with object identity (Burwell et al., 1998). What makes the hippocampus an ideal structure of making arbitrary associations among items and places is the CA3's autoassociative network composed of recurrent collaterals (Marr, 1971; McNaughton and Morris, 1987; Ishizuka et al., 1990; Treves and Rolls, 1994; Amaral and Witter, 1995; Hasselmo et al., 1995; Rolls et al., 1998; Kesner et al., 2001). The recurrent collateral fibers of CA3 pyramidal neurons connect CA3 neurons extensively with each other and the information represented in a subset of CA3 neurons can make arbitrary and rapid associations with other information represented in other neurons (Marr, 1971; Hopfield, 1982; McNaughton and Morris, 1987; Mizumori et al., 1989; Hasselmo et al., 1995; Rolls et al., 1998; Kesner et al., 2001). There are some studies that have examined the associative function of the hippocampus (especially CA3) using single-unit recording or lesion techniques in mnemonic

settings and we will provide selective review on some of the studies in the following sections.

## SINGLE-UNIT RECORDING STUDIES

Rolls (1989) conducted an electrophysiological study with monkeys on this issue. In that study, monkeys performed an object-place association task in which they were required to judge whether a particular visual stimulus was presented in a certain location in which the stimulus had previously been presented. As the monkeys performed this task with various stimuli, some neurons in the hippocampus fired only when a certain stimulus was seen in a particular location, but not in other positions (Rolls, 1989). The results support the hypothesis that some hippocampal neurons respond to objects and their associated locations in a combinatorial fashion.

Komorowski recorded hippocampal neurons while rats performed odor-context associations (Rolls, 1989; Komorowski et al., 2009). In that study, main components of an event were a cup filled with sand (scented with a particular odor) and its location in a certain compartment of a chamber. There were two cups with different odors and there were two compartments (or contexts) with the walls of each compartment associated with either black or white color. The task was a biconditional task because one of the odors rewarded in a certain context was not rewarded in the other context, and vice versa for the other odor. This study addresses this issue to some degree by showing changes in the responsiveness of hippocampal neurons as learning proceeded for the item in context. According to their result, cells that fired in association with item-position variables gradually appeared during training while place cells in the hippocampus remain consistent in their firing rate throughout the training. Furthermore, the activation of these item-position selective cells can predict performance accuracy. However, this task may not be testing the role of context because it was not necessary for the rats to pay attention to the contextual information since the rat left a given compartment voluntarily to enter the opposite compartment. In a sense, spatial information could be obtained during the alternation between compartments without the contextual information (i.e., wall color of each compartment).

Information about the external world enters the hippocampus by various routes and the entorhinal cortex and the PER are considered important upstream structures of the hippocampus in this regard. Knowing physiological characteristics of neurons in these upstream structures is thus very important in understanding the hippocampal mechanisms for event information processing. Suzuki tested firing properties of cells in the PER and entorhinal cortex in object recognition memory (Suzuki et al., 1997). Monkeys performed two different behavioral tasks. One was a delayed-matching-to-sample task (DMS), which tested whether monkeys could remember previously seen objects by choosing it later when several objects were shown sequentially. Another task was a delayed-matching-to-place task (DMP) in which monkeys must choose a visual cue on the screen only when it appeared in a location that was previously associated with the cue. In the DMS task, entorhinal cortical cells showed different responses to the test stimuli depending on whether they match sample stimuli, which means that the entorhinal cortex is involved in processing object recognition memory. In addition, entorhinal cortical neurons also showed stimulus-specific activity during delay, which was also shown in the PER where a large proportion of cells showed object-specific responses. In the DMP task, entorhinal cortical cells showed different responses depending on the location of a cue on the screen (Rolls, 1989). Thus, this study supports the hypothesis that the entorhinal cortex processes sensory information associated with objects and their spatial locations, both of which may be used in the hippocampus to form event memory.

The Suzuki group also recorded neuronal activity in the hippocampus and the PER. Monkeys were required to remember multiple locations each of which was associated with a particular scene and PER cells showed firing correlates with learned spatial-scene association. This study supports that the PER is not only involved in object information processing but also in spatial-context association to some degree.

On the other hand, spatially selective neuronal firing was observed in the POR as compared to the spatial firing of hippocampal neurons (Burwell and

Hafeman, 2003). Although the firing properties of the MEC and PER cells have been examined with electrophysiology, the firing characteristics of the cells in the POR have never been investigated before the Burwell group recorded neuronal responses in the POR. In a four-arm radial maze, rats were tested in three conditions: baseline, double-cue rotation (proximal +90 degree; distal -90 degree), the second baseline. Although POR cells showed spatially correlated neuronal firing, firing patterns were different from those of hippocampal place cells. The POR neuronal firing fields were correlated more with the changes in the visual cues in the environment and were less correlated with stable space in the environment. This may mean that the POR is an earlier step of processing visuo-spatial information which supposedly helps the hippocampal neurons to create stable place fields. Therefore, this study supports the hypothesis that the POR contributes to forming event memory in the hippocampus by providing spatial information.

## LESION STUDIES

Some lesion studies also investigated object-place associative memory. For example, Gaffan hypothesized that macaque monkeys associate spatial representation with object representation and called it "object-place configural memory" on the basis of three experiments (Gaffan, 1994). In the first experiment, monkeys were required to learn the followings: If objects A and B covered two food wells in a Wisconsin General Test apparatus, then food reward was found in left food well regardless of the position of A or B, whereas objects C and D signaled that food reward was in right food well (Gaffan, 1994). Therefore, the spatial memory of finding reward on the left food well was associated with objects A and B. Conversely, in spatio-visual conditional learning monkeys were required to associate objects shown in the test with locations. For example, if objects E and F were both on the left (in a tray with two food wells on both sides), then only E was rewarded, while if they were both on the right, only F was rewarded (Gaffan and Harrison, 1989). Object-place memory was also tested in a recognition memory test in which some

particular objects appeared in specific locations (Gaffan et al., 1985). Here, a monkey saw a particular object in a particular place and was later able to indicate whether the test object was presented in the same place. In all three experiments, monkeys with fornix transections or hippocampal aspiration lesions showed deficits in associating objects and places together.

Gilbert and Kesner (2002) also examined object-in-place memory by using a biconditional paired-associate memory task. In their Go/No-Go task, choosing a particular object A in location 1, but not in location 2, was rewarded whereas choosing an object B in location 2, but not in location 1, was rewarded. Rats with hippocampal lesions showed severe deficits in acquisition and retention of this task. Especially CA3, a subfield of the hippocampus, appears to be important in the acquisition of this task because of its associative function (Marr, 1971; McNaughton and Morris, 1987; Gilbert and Kesner, 2003; Rolls and Kesner, 2006).

Eacott and Norman (2004) suggested a model of episodic-like memory for rats. In their task, rats were tested for their integrated memory for object, place, and context. The animals were presented with two familiar objects and only one of them was not in its previous location and context (both location and context were familiar to them) (Eacott et al., 2004). Rats preferred a novel configuration than familiar one, which means they were able to integrate object, place, and their associated context. Perirhinal cortical lesions did not impair object-place memory (Ennaceur et al., 1996) and caused relatively mild, delay-dependant impairments of object-context memory (Eacott et al., 2004). On the other hand, POR lesions impaired memory for object-context associations more severely than fornix lesions (Eacott et al., 2004). Therefore, fornix lesions produced impairment by disrupting the configuration of object, place, and context rather than by disrupting one of these elements.

The lesion studies mentioned above, however, may never reveal the mechanisms of object-place paired association in the medial temporal lobe because those studies never test how the normal brain works. Therefore, electrophysiological studies are needed. Recent electrophysiological studies (Lee et al., 2004; Leutgeb et al., 2004; 2005) have

reported that hippocampal subfields (DG, CA3, and CA1) are important when ambiguity in the environment needs to be processed. However, these studies were carried out using non-mnemonic behavioral paradigms such as foraging for food pellets as the environment underwent changes for inducing contextual ambiguity to the animals. In other words, the animals were not required to use the changed, ambiguous contexts to solve a certain memory problem in those studies.

### **DISAMBIGUATION OF COGNITIVE REPRESENTATIONS FOR EVENTS IN THE HIPPOCAMPUS**

To investigate how the hippocampal subfields process ambiguous event information to store them as discrete representations, we have used an object-place paired-associate task. Before conducting electrophysiological investigations, we performed several lesion/inactivation studies to learn the functions of the hippocampus and its associated regions.

In our study, an object pair was presented in two different places of a radial-arm maze and each object within the pair was associated with reward only in a particular arm of the maze. Therefore, as the same pair of objects was presented in two different locations, the animal needed to form discrete object-place paired associates and their reward values. Since some of these conditions share the same elements (such as same objects and maze arms) but each condition could be remembered as a distinct event, this task requires the rats to disambiguate similar event representations. In the hippocampus, the dentate gyrus (DG) is known for its role in pattern separation of similar places (Leutgeb et al., 2007) and CA3 is widely known for its role in auto-association among items (Rolls and Kesner, 2006), which enables various kinds of information to become bound together. These two subfields are supposedly very important in our task since both arbitrary associations between object and places, and the orthogonalization of similar spatial locations (different arms of the maze) needed to occur at the same time.

In our previous study (Lee, 2008; Lee and Solivan, 2008), we showed that the hippocampal

lesioned rats as well as the rats with lesions in the DG were impaired not only in the retention of object-in-place memory but also in the acquisition of the memory as compared to the control lesioned group. These results confirm that the hippocampus (especially the DG) is necessary for detecting differences between similar events in which object and place need to be associated as discrete event representations. However, rats with lesions in the PER showed recovery in performance for remembering previously learned paired associates, whereas the lesioned rats showed total deficits for learning new paired associates. When the task required rats to just discriminate different objects within the same arm, the impairment disappeared in all three lesions (i.e., hippocampal, DG, and perirhinal cortical lesion) groups, which means that none of these areas may be necessary for just simple object discrimination. We describe results from these and other studies from our laboratory in more detail below.

### **HIPPOCAMPAL CONTRIBUTION TO THE DISAMBIGUATION OF SPATIAL CONTEXT**

In one of our studies (Kim and Lee, 2010), rats with dorsal hippocampal lesions or pharmacological inactivations were severely impaired in disambiguating similar spatial contexts. In this task, rats were trained to associate two different configurations of distal cue-sets (i.e., spatial context) with different food-well locations. We found that hippocampal lesioned rats were unable to retrieve the context-place paired associations learned before surgery. We also found that rats with muscimol inactivation in the dorsal hippocampus were unable to discriminate ambiguous contexts composed of modified spatial contexts (by varying the angular distance between distal cue sets). These results suggest that the hippocampus is necessary for spatial discrimination using distal cue-configuration, especially when the distal cue-configurations are similar to each other.

### **HIPPOCAMPUS AND DG ARE NECESSARY FOR DISCRIMINATING SIMILAR OBJECT-PLACE PAIRED ASSOCIATIVE EVENTS**

To test the role of the hippocampus in disambiguating similar object-place associations, Lee and Solivan (2008) used a radial-arm maze surrounded by black curtains and there were visual cues that provided rats with spatial or contextual information on the curtains. When a trial began, the rat was placed in the start box on the center platform. One of two arms (arm 3 or arm 5) was opened by an experimenter and the animal entered the opened arm. At the end of the arm, there was a so-called 'event platform' and the rat saw two objects in the event platform. Each object was positioned on top of a food well in which a small cereal reward was hidden. The rat needed to displace one of the objects to obtain reward. Choosing a certain object was rewarded in arm 3 and choosing another object was rewarded in arm 5. Thirty-two trials were given per day during training and when the rat reached performance criterion (75% correct performance in both arms for two consecutive days) they received lesions in the hippocampus. After a week of recovery period, rats were tested again in the same task. Hippocampal lesioned animals were severely impaired in the task (Lee and Solivan, 2008), suggesting that the hippocampus is crucial in processing object-place associations especially when there is ambiguity due to overlapping components between events.

Rats with lesions in the dorsal DG also demonstrated deficits in the same task described above (Lee & Solivan, in press). However, if the ambiguity was removed by using non-overlapping objects between different arms in the maze (Experiment 2) or by presenting objects in the arms more separated from each other (Experiment 3), the DG lesioned rats performed normally (Experiment 2) or relearned the task (Experiment 3). These results suggest that the DG is necessary for amplifying small differences among similar object-place paired associates to produce more distinctively different neural representations. The DG appears to be more important when the same objects were presented at closer locations, which

means DG is important for spatial pattern separation (Leutgeb et al., 2007). However, the DG lesion animals never showed the level of performance demonstrated by the control group and this suggests a possibility that the DG might be also important for disambiguating nonspatial components such as same objects associated with different spatial locations. Furthermore, when there was no object similarity in experiment 2, DG lesion rats were unimpaired. In addition, the perirhinal cortex (PER) is necessary for acquiring novel object-place paired association but not in retrieving old one. When the rats with lesions in the PER performed the same task learned before surgery, they showed impairment during the early days of testing period (Jo and Lee, 2010). However, the performance improved in later part of testing and this suggests that the PER is originally involved in retrieving well-learned object-place paired associative representations but is not necessary because it appears that other areas may take over the function. We then became interested in whether the PER is more important for “forming” new associations between object and place information. To test this, rats were tested in the same object-place paired-associate task except that novel objects were used this time. The PER lesion group was unable to learn the newly introduced paired associations. These results overall indicate that the PER is necessary for novel object-place paired association and no other area can take over this unique function of the PER in this domain.

## DISCUSSION

The object-place paired-associate task we have used to assess the roles of the hippocampus, DG, and PER is an ideal behavioral paradigm to gain insights into the functions of medial temporal lobe structures. In future studies, it is necessary to gain more mechanistic understandings of individual circuits in the hippocampus and its associated regions. Most of all, it is yet to be determined whether the mechanisms underlying the impairment of the lesioned animals come from deficits in spatial information processing, nonspatial information (e.g., object) processing, and/or the conjunction of object and space information. For example, when the

DG-lesioned animals exhibited deficits in the task (Lee & Solivan, in press), it could be purely due to impairment in spatial pattern separation between different locations in space. Confirming this hypothesis would require showing impaired performance when purely spatial discrimination is necessary, but normal performance when such spatial requirement is removed in the task. Our previous study (Lee & Solivan, in press) did not test animals in a purely spatial condition and future studies may address the issue with electrophysiological techniques. For a purely spatial test, no object should be used during the test and the results should be compared to object-place paired associative test. It would be also necessary to test animals in a situation where many different or similar objects need to be discriminated in the absence of spatial information.

A leading hypothesis suggests that there are two main information-processing streams leading to the hippocampus (Burwell et al., 1998). One is the PER → LEC → hippocampus stream, which may process nonspatial information (individual sensory stimuli such as objects and odors), and the other is the POR → MEC → hippocampus, which involves spatial information processing. The PER may be necessary for discriminating similar objects and retrieving previously formed object memory. In our PER lesion study, rats with PER lesions were able to perform previously learned task as time passed, but showed deficits in acquiring new paired associates between objects and places. It may be that the PER contributes to forming pattern-separated representations of object-place paired associates and once such representations are formed, the area is no longer necessary and other areas such as the LEC may take over the function of retrieving old memory representations.

Some of the results of our lesion studies may not be consistent with classical theories that assert that the hippocampus is the place where spatial and non-spatial information are bound together for the formation of an event memory. According to prevalent view, two types of information, spatial and non-spatial information, are processed in separate pathways and these inputs are combined at the hippocampus level. However, our lesion studies suggest some interesting points that may not be

perfectly explained by the previous theories. First of all, in our study, DG-lesioned rats showed some additional effects of object-information processing even when the load for spatial information was reduced significantly. This suggests that the DG may play a role in combining the object information with the spatial information in the object-place paired-associate task. There has been no evidence for proving or disproving that the DG is involved in processing object and place information together and our study investigated the issue for the first time. Second, rats in our study could not learn new object-place association after PER lesion while showing gradual improvement in performance for old object-place paired-associates in the object-place paired-associate task. The perirhinal cortical lesions did not impair the performance in the simple object discrimination task. The results suggest that the perirhinal cortex is not only sensitive to object information but also processes spatial information particularly if the spatial information is critical in assessing the identity of an object. Given the strong feedforward inputs from the POR to the PER, it may be that at the PER and POR level, the spatial and nonspatial information may be combined to some degree and likewise at the MEC and LEC level. These results imply that the hippocampus may not be the first place where spatial and nonspatial information are combined together. Anatomical studies also show that the POR projects to the LEA and the PER projects to the MEA (Van Strien et al., 2009). Furthermore, extensive connectivity between PER and the POR, MEA and LEA were also found (Van Strien et al., 2009). In addition, the entorhinal cortex and the hippocampus are also anatomically interconnected (Lingenhohl, 1991; Witter, 1993). Electrophysiological studies recording multiple single units simultaneously from different regions in the medial temporal lobe should shed a light on these issues in future studies.

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