ABSTRACT: A non-navigational test of incidental spatial learning was used to determine whether hippocampal damage causes temporally-graded retrograde amnesia (TGRA) for allocentric-spatial information. Rats were exposed to two identical objects in a circular open field for 7 min on seven consecutive days. In the 1–3 days after the last day of familiarization, rats received neurotoxic lesions of the hippocampal formation (HPC) or sham lesions. Another two groups received the same lesions 3 weeks after familiarization. The rats were then placed back in the open field with one object displaced, and the time spent in each of the quadrants as well as time spent exploring the objects was recorded. Rats that received HPC lesions 3 weeks but not 1–3 days after familiarization showed evidence of preserved remote spatial memory; however, their remote memory was expressed through different behavior than control rats. Rats with HPC lesions spent more time with the displaced object than with the object that remained in the same place, whereas control rats spent more time in the quadrant where the displaced object used to be. These results suggest that remote spatial memories may be preserved with a sufficiently long familiarization-to-surgery interval before HPC lesions, but that the nature of these memories may differ in quantity and/or quality from those of intact rats. © 2009 Wiley-Liss, Inc.

KEY WORDS: memory consolidation; novelty preference; open field; exploration; place preference

INTRODUCTION

Memory consolidation refers to a hypothesized process by which memories initially stored in a labile state are gradually stabilized in a more permanent form in the brain. In what has become known as the standard model, newly acquired memories are initially dependent on the hippocampus for retrieval as they are gradually stored in the neocortex over time (Squire, 1992; Squire and Alvarez, 1995). Once this process concludes these memories are no longer dependent on the hippocampus. Support for this idea comes from observations of TGRA in which memories acquired recently before hippocampal damage are lost whereas memories acquired at more remote time periods are preserved. This pattern of memory loss has been observed in humans (Scoville and Milner, 1957; Rempel-Clower et al., 1996; Reed and Squire, 1998; Kapur and Brooks, 1999; Teng and Squire, 1999), monkeys (Zola-Morgan and Squire, 1990), and rodents (Kim and Fanselow, 1992; Maren et al., 1997; Anagnostaras et al., 1999; Winocur et al., 2001; Tse et al., 2007).

Department of Psychology, Center for Studies in Behavioural Neurobiology, Concordia University, Montreal, Quebec, Canada H4B 1R6
*Correspondence to: Stephane Gaskin, Department of Psychology, Center for Studies in Behavioural Neurobiology, Concordia University, Montreal, Quebec, Canada H4B 1R6. E-mail: sgaskin@alcor.concordia.ca
Accepted for publication 20 January 2009
DOI 10.1002/hipo.20583
Published online 17 March 2009 in Wiley InterScience (www.interscience.wiley.com).

There is controversy over whether remote memories are preserved because they become independent of the hippocampus or because more traces have become associated with them. (Nadel and Moscovitch, 1997; Frankland and Bontempi, 2005). These traces may be spread throughout the entire hippocampus resulting in preserved remote memories when damage to the hippocampus is incomplete. Within this framework, TGRA should only occur with partial hippocampal damage. With complete lesions, both recent and remote memories should be equally affected, resulting in ungraded retrograde amnesia (Sanders and Warrington, 1971; Mumby et al., 1999; Viskontas et al., 2000; Cipolotti et al., 2001; Sutherland et al., 2001; Gaskin et al., 2003; Lehmann et al., 2007; Sutherland et al., 2008).

In cases where complete lesions lead to TGRA, Nadel and Bohbot (2001) suggested that seemingly spared remote memories may reflect the retrieval of memories that are qualitatively or quantitatively different from memories acquired by the hippocampus. Consistent with this idea, Kubie et al. (1999) found that rats can remember the spatial location of food in a dry version of the Morris water-maze task with a long, but not a short training-to-surgery interval. However, when the long-interval rats were re-tested they were unable to use the seemingly consolidated information to solve a new problem in the same maze, whereas sham rats were successfully able to use information acquired during training and found the food situated in a new location. These authors suggested that, with a damaged hippocampus, remote spatial memories in rats might be retrieved as vector based representations (Alyan and McNaughton, 1999; Hamilton et al., 2004) that can support some aspects of navigation. However, these memories are not as efficient as the map-like representations (O’Keefe and Nadel, 1978) characteristic of normal rats. Nadel and Bohbot (2001) have also interpreted recent findings, in which evidence of spared remote spatial memories in humans and rodents was found. They point out that these memories were qualitatively and quantitatively different than the same memories observed in normal subjects (Bontempi et al., 1999; Rosenbaum et al., 2000).

Another issue concerns the lack of TGRA in studies involving the Morris water-maze. One common explanation for this is that a functional hippocampus is required for navigation, or other on-line processes,
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FIGURE 1. Spatial Novelty Detection: In this paradigm, rats’ spatial memories can be expressed and assessed in multiple ways: the time spent exploring the displaced object vs. the object that remained in the same location (displaced vs. nondisplaced), the time spent exploring the entire quadrant in which an object was displaced to vs. the quadrant where an object always was (new/same) or the time spent exploring the entire quadrant from which an object was displaced from (where an object used to be) vs. where an object never was (former/never). A) Object configuration during familiarization and B) Object configuration with one object displaced to another quadrant during the test.

during the test (Riedel et al., 1999; Clark et al., 2005a, b). This requirement implies that water-maze tasks may be severely limited in their ability to inform us about the effects of hippocampal damage on long-term memory consolidation.

In the present study, we tested rats in a non-navigational place-learning test, which takes advantage of rats’ ability to detect spatial changes in their environment. This test is a variant of a set of well documented tests in which rats display an ability to detect spatial changes in their environment (Pouget et al., 1986; Thinus-Blanc et al., 1987; Pouget, 1989; Thinus-Blanc et al., 1991; Mumbly et al., 2002; Good et al., 2007) and in which they are impaired by hippocampal lesions (Save et al., 1992a, b; Mumbly et al., 2002; Good et al., 2007). The detection of this change is inferred if rats spend more time exploring a displaced object rather than an object that has remained stationary.

The main difference between the version of the test in the present study and the tests used in previous studies (Pouget et al., 1986; Thinus-Blanc et al., 1987; Pouget, 1989; Good et al., 2007) is that one of only two objects is displaced in a large circular open field surrounded by several extra-maze cues. This is an important difference from previous studies in which one of several objects was displaced. In these studies, the tests emphasize the detection of a change in the topological relationships of the objects relative to one another and not necessarily to distal spatial cues in the environment. Nevertheless, one key element of the test used in the present study, shared with tests that use multiple objects, is that it does not require navigation.

Another important difference lies in the exploratory behaviors measured in the present test, compared to previously-described tests. During pilot experiments, we found that it was possible for rats to display several types of exploratory preferences, each of which, can indicate that a rat has detected a spatial change in the environment. Therefore, in the present study, memory for the previous location of an object was inferred if rats either: (1) spent more time exploring the displaced object vs. the nondisplaced object, (2) spent more time in the quadrant in which the object was displaced vs. the quadrant containing the nondisplaced object, (3) spent more time in the quadrant that previously contained the displaced object vs. the quadrant that was previously empty and remained empty for the test.

We hypothesized that if TGRA is not observed with the use of spatial tasks because of their navigational nature (Riedel et al., 1999; Clark et al., 2005a, b), and that if HPC-dependent spatial memories undergo systems consolidation, then testing rats that received postfamiliarization lesions of the HPC, in a non-navigational test of spatial learning should result in TGRA. In this test, rats were given multiple familiarization trials during which they were permitted to explore a circular open-field arena containing two copies of an identical object, each object situated in the center of two adjacent quadrants. Subsequently, the rats were placed back into the arena, with one of the objects displaced to the center of a previously empty quadrant. The time spent in each quadrant, and time spent investigating each of the objects was recorded.

METHODS

Subjects

Subjects were 30 male Long-Evans rats (Charles River, St-Constant, Quebec, Canada) weighing 420–590 g at the beginning of the study. The rats were housed individually in standard shoe-box cages under a reverse cycle (8:00/20:00). The rats had continuous access to food (standard lab chow; 507-U.S. Charles River Rodent) and water. All procedures were approved by the Concordia University Animal Care and Use Committee, and were in accordance with the guidelines of the Canadian Council on Animal Care.

Apparatus and Materials

The apparatus, illustrated in Figure 1, was a circular open field (137 cm in diameter and 46 cm high) previously used for
Morris Water Maze testing (Morris, 1982). It was located in the center of a room containing various extra-maze cues. A white circular cut-out of corrugated plastic covered the entire floor of the open field. Stimulus objects (6 cm high) were made of glazed ceramic with a small glass jar (6 cm high) glued to the bottom with epoxy resin. The lids to the jars were fastened to the corrugated plastic covering the floor of the open field. The objects were secured into place by screwing the jars into the lids. The objects were separated by 61 cm from center to center and each object was situated approximately 35.6 cm from the sides of the open field closest to them. Holes were drilled at the center of each of the quadrants to accommodate the lids and to permit the counterbalancing of the position of the objects. When not in use the holes were covered with a small white circular tape.

The use of a large open field to test the displacement of one of two objects in our laboratory stems from unpublished data, using a much smaller square enclosure, which has yielded inconsistent results, with several groups of rats failing to demonstrate an exploratory preference for the displaced object. This may have been due to not being able to produce a big enough change in absolute spatial location within a small enclosure to be detected by the rat. This led us to conduct the test in a large circular open field, a dry water-maze. Using this apparatus, a much larger displacement of the test object could be made.

**TABLE 1.**

<table>
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<tr>
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<th>Mediolateral (ML)</th>
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**PROCEDURE**

Presurgery Habituation and Familiarization

Rats were brought to a waiting room adjacent to the test room, which was used for all phases of the experiment. The rats were brought to this room in their home cages and remained there for 30 min before each habituation, familiarization and testing session. Habituation consisted of placing the rat in the middle of the arena with no object present and permitting it to explore for 5 min.

Familiarization began 24 h after habituation. Objects were fastened into place and rats were permitted to explore the open field (Fig. 1A) for 7 min/day for seven consecutive days. On every trial the experimenter placed the rat in the center of the open field facing away from the objects. The position of the objects was counterbalanced to control for the possibility that some rats preferred one area of the open field over another. The apparatus and objects were thoroughly cleaned with a 70% alcohol solution after each habituation, familiarization and test trial. A video camera located directly above the center of the open field was used to record familiarization and test sessions.

Surgery

Rats received surgery either 1–3 days or 3 weeks after the last day of familiarization (RECENT and REMOTE conditions, respectively). Rats were subjected to N-methyl-D-aspartate (NMDA [Sigma Chemical, St-Louis MO]) lesions of the hippocampus ([HPC-RECENT] n = 8), ([HPC-REMOTE] n = 7) or Sham surgeries (SHAM-RECENT) n = 8), (SHAM-REMOTE) n = 7). Table 1 shows the coordinates, based on Paxinos and Watson (2005), used for the lesions. The objective was a lesion that damaged both the dorsal and ventral HPC. Rats were anesthetized with 3% isoflurane (Janssen, Toronto, Ontario, Canada) in 0.08 l/min of oxygen at 41.7 psi at 21°C (Benson Medical Industries, Markham, Ontario, Canada). Animals in the HPC groups were infused with NMDA (7.5 μg/μl) at the rate of 0.15 μl per minute for a total volume of 0.45 μl at 10 sites per hemisphere. The injections were made through an injection cannula attached to PE-20 tubing using 10-μl Hamilton syringes mounted on a micro-injection pump. The injection cannula was left in the injection site for 2.5 min after the injection to facilitate diffusion of the drug. All the rats received an injection of diazepam (0.2 cc; 10 mg/ml, i.p; Hoffman-La-Roche, Mississauga, Ontario, Canada) as a prophylaxis against seizures. All rats in the SHAM groups were subjected to the same procedure with the exception that no damage was done to the skull and no drug was infused in the brain. Behavioral testing for all rats started after 15 days of recovery.

Postsurgery Testing

After recovery, the rats were brought back to the waiting room for the usual 30-min wait while the experimenter fastened the objects to the floor of the arena. However, this time one of the objects was repositioned to the center of the opposite quadrant (Fig. 1B). The rats were then placed in the center of the maze, facing away from the objects, and permitted to explore the open field for 5 min. The time spent in each of the quadrants as well as the time spent exploring each object was recorded. The time spent in a quadrant that contained an object included the total time spent exploring the object and the time spent in the rest of the quadrant. A rat was considered to be exploring an adjacent quadrant if its head crossed over to

*Hippocampus*
an adjacent quadrant, determined by the presence of crosshairs on the television screen used for scoring. Rats were considered to be investigating an object as soon as they came within two centimeters of the object while being oriented directly towards it. Rats were also considered to be investigating the object if they reared and touched it while looking elsewhere in the testing room.

The dependent measures for quadrant exploration were (1) the comparison between the average time spent exploring the quadrant where an object was moved to (NEW) vs. the quadrant in which the other object remained (SAME). (2) The comparison between the quadrant from which an object was displaced from (FORMER) vs. the quadrant that never contained an object (NEVER). The main dependent measure for object investigation was the proportion of time spent exploring the displaced object vs. the nondisplaced object \[\frac{t(\text{Disp.})}{t(\text{Disp.}) + t(\text{Undisp.})}\].

**Histological Results**

Figure 2 illustrates the extent of the hippocampal lesions. The NMDA injections produced extensive cell loss in all principle subfields of the hippocampus and dentate gyrus. All rats had substantial damage to the subiculum. No damage to the entorhinal and perirhinal cortices was found.
Quantification of Hippocampal Lesions

The extent of hippocampal lesions at four coronal planes of section (AP −2.5, −5.2, −5.8, −6.8) for each rat were traced onto images taken from a rat brain atlas (Paxinos and Watson, 2005). The images were then scanned into Corel Draw®. The area covered by the lesion at each section and on each side of the brain was compared to the area covered by the hippocampus by dividing the number of pixels within the lesioned area by the number of pixels within the confines of the hippocampus.

Lesions in the HPC-RECENT group averaged 79% of the total hippocampus, vs. 72% in the rats in the HPC-REMOTE group. All rats except for one in the HPC-REMOTE group had extensive bilateral damage ranging from 90 to 100% of the dorsal-most part of the hippocampus (AP −2.5) and 80 to 100% in the medial-most area (AP −5.2). Most sparing occurred in the posterior-most parts of the hippocampus (AP −5.8 and −6.8). There was some sparing of 20% of the ventral-most part of the hippocampus in six rats in the HPC-RECENT condition and in five rats in the HPC-REMOTE. Two rats in the HPC-RECENT condition had more extensive damage in their right vs. left hippocampus.

Time Spent in Quadrants During Testing

Two-way mixed design analyses of variances (analysis of variance (ANOVA)), with Lesion-group (SHAM and HPC) as the between subjects factor and Quadrant-time as the within subject factor, were performed for both the Recent and Remote conditions. The dependent measures were then evaluated using planned comparisons (Tukey HSD) to compare the cumulative time spent between the two object-quadrants and between the two no-object quadrants. In addition, one-sample t-tests comparing the rats’ object preference to chance (50%) were conducted.

The ANOVAs revealed a significant main effect of Quadrant-time for both the Recent [F (3,48) = 10.34, P < 0.0001] and Remote [F (3,42) = 4.44, P < 0.009] conditions. There was no significant Lesion-group or Lesion-group X Quadrant-time interaction effects.
Figure 4A shows the average time spent in each of the quadrants during the first two cumulative minutes of testing for rats in the SHAM-RECENT and HPC-RECENT conditions. Figure 4B shows the average time spent in each of the quadrants during the first two cumulative minutes of testing for rats in the SHAM-REMOTE and HPC-REMOTE conditions.

Rats in the SHAM-RECENT group [F (1,48) = 6.1542, \( P < 0.01 \)], but not in the HPC-RECENT group [F (1,48) = 0.770, p = n.s.], spent significantly more time in the NEW vs. the SAME quadrant whereas rats in the SHAM-REMOTE group [F (1,42) = 4.81, \( P < 0.01 \)], but not in the HPC-REMOTE group [F (1,42) = 0.830, p = n.s.], spent significantly more time in the FORMER vs. the NEVER quadrant.

To further assess whether rats in the HPC-REMOTE group displayed signs of preserved memory for the previous location of the displaced object, investigation ratios for the HPC-RECENT and HPC-REMOTE rats were compared to chance (50%) using one-sample \( t \)-tests.

Figure 5A,B show object investigation ratios \([t(\text{Disp.}) / t(\text{Disp.}) + t(\text{Undisp.})]\) for the first and first two cumulative minutes for the rats in the RECENT and REMOTE conditions respectively. One sample \( t \)-tests revealed investigation ratios for the first, and first two cumulative minutes, that were not different from chance for rats in the HPC-RECENT group, but were significantly above chance for the rats in the HPC-REMOTE group (first minute \([t(6) = 3.356 \, P < 0.007] \) and (first two minutes \([t(6) = 2.036 \, P < 0.044] \).

**DISCUSSION**

The main finding was that rats in the HPC-REMOTE condition showed some evidence of spared spatial memory, as indicated by object investigation ratios that were significantly above chance, whereas rats in the HPC-RECENT condition did not show any evidence of preserved spatial memory. Evidence for intact spatial memory was found for the rats in both the SHAM-RECENT and SHAM-REMOTE conditions. This finding is consistent with the standard model of memory consolidation (Squire and Alvarez, 1995), which states that memories are initially dependent on the HPC but gradually become consolidated in the neocortex over time. However, as a cautionary note to the reader, the results may somewhat be limited by the absence of a significant group effect across the time spent in each of the quadrants for both the RECENT and REMOTE conditions. Nevertheless, the separate comparisons of investigation ratios between HPC-RECENT and HPC-REMOTE rats against chance are compelling.
The displacement of a single object for the test gave rise to three novel situations: a previously empty quadrant that now contained an object, a quadrant that previously contained an object and was now empty, and an object that now had a new location relative to spatial cues in the environment. It was therefore possible for rats to express memory for the spatial location of objects in several ways: (1) SHAM rats in the RECENT condition expressed their memories for the previous location of the displaced object by spending more time in the quadrant in which an object was displaced to (new) for the test than in the quadrant that also contained an object during familiarization (same). They did not spend more time investigating the displaced object than the object that remained in the same location. (2) SHAM rats in the REMOTE condition spent more time in the quadrant that contained the object during familiarization, but that was empty during the test (former), than in the quadrant that never contained an object (never), but not in the quadrant in which the object was displaced to for the test (new). They did not spend more time with the displaced object vs. the object that remained in the same location. (3) Rats in the HPC-RECENT condition did not display any of these preferences, suggesting impaired memory for the previous location of the displaced object. (4) Rats in the HPC-REMOTE condition displayed preferential investigation of the displaced object vs. the object that remained in the same location suggesting the possibility that some form of expression of memory for the previous spatial location of that object remained intact. This finding raises the possibility that when hippocampal lesions were performed 3 weeks after familiarization, as in the HPC-REMOTE rats, that at least some aspect of the memory for the previous spatial location of the object was preserved by becoming independent of the hippocampus, a possible example of TGRA.

TGRA in rats was found in studies that involved lesions to various components of the hippocampal system such as the perirhinal cortex (Wiig et al., 1996), entorhinal cortex (EC) (Cho and Kesner, 1996) fornix (Wiig et al., 2001) and subiculum (Bolhuis et al., 1994). Of the studies in which lesions restricted to the HPC were made (Winocur, 2001; Kim and Fanselow, 1992; Maren et al., 1997; Ramos, 1998; Anagnostaras et al., 1999; Winocur et al., 2001; Tse et al., 2007) some involved only the dorsal hippocampus (Winocur, 1990; Maren et al., 1997; Ramos, 1998; Anagnostaras et al., 1999).

Only one study (Tse et al., 2007) showed TGRA of spatial memory with complete HPC lesions. One reason for the lack of a temporal gradient in most previous studies exploring retrograde spatial memory may be that the hippocampus is needed for navigational performance (O’Keefe and Nadel, 1978) in the tasks that were used to assess spatial learning. On the other hand, Tse et al. (2007) suggested that systems consolidation of spatial memories is possible if rats learn an associative schema of the spatial information used in a subsequent test. However, in that study the training-to-surgery interval of only 48 h does not discount the possibility that cellular and non-systems consolidation occurred. Cellular consolidation involves molecular changes that strengthen memories in local circuits. The time frame associated with this process is on the scale of hours (Debiec et al., 2002), whereas the time frame associated with systems consolidation in rats is days or months (Winocur, 1990; Kim and Fanselow, 1992; Kim et al., 1995; Maren et al., 1997; Ramos, 1998; Anagnostaras et al., 1999; Winocur et al., 2001). The temporal gradient observed in the study by Tse et al. (2008) may have been due to the disruption of cellular consolidation in other brain areas. This idea is now being debated (Rudy and Sutherland, 2008; Tse et al., 2008) but there is evidence that the excitotoxic lesions may affect immediate early gene expression in areas outside the infusion site (Glenn et al., 2005).

One factor that may account for the lack of TGRA for spatial memory in previous studies could be the differences between the test used in the present study, and the tasks often used to assess retrograde spatial memory in rats: (1) the test in the present study is non-navigational, (2) learning in this test is incidental and does not rely on the use of reward or punishment and, (3) the assessment of spatial memory can be performed using several measures that do not all relate to a single factor, such as the location of a hidden platform in a open field of water (Morris, 1982) or the retrieval of food from the arms of a maze (Olton and Papas, 1979).

In navigational tasks such as the ones often used in a pool of water (Morris, 1982), rats may require normal hippocampal function to keep track of the relationships between spatial cues in their environment to update their location in relation to the platform location during the test (O’Keefe and Dostrovsky, 1971; O’Keefe and Nadel, 1978; O’Keefe and Speakman, 1987). An intact HPC may also be necessary for dead reckoning (Wallace and Whishaw, 2003), a navigational strategy in which rats can estimate their present location in relation to a starting point (Whishaw, 1998). In the present study we used a test that takes advantage of rats’ natural propensity to explore novelty. In this test, novelty is reflected as a spatial change in the position of one of the objects relative to distal spatial cues situated in the environment surrounding the open field. It is not expected that this behavior requires navigation, which may exclude the necessity for an intact HPC during the test.

**Alternative to the Standard Model**

The multiple-trace theory proposed by Nadel and Moscovitch (1996) proposes that the hippocampus is always involved in the storage and retrieval of episodic memories regardless of their age. They suggest that whether TGRA occurs or not depends more on the size of the hippocampal lesion than the age of the memories. According to these authors more remote memories have a better chance of being preserved because more traces have been associated with them than more recent memories. The number of preserved traces available for the retrieval of memories is reduced as the size of the lesion increases, with very large or complete lesions giving rise to a flat gradient of memory loss, in which both recent and remote memories are equally affected.

When large or complete hippocampal lesions lead to TGRA, Nadel and Bohbot (2001) suggested that what is taken to be
consolidated remote memories may be memories that were never dependent on the hippocampus for their storage or retrieval. They suggest that in patients with hippocampal damage what seems to be spared remote spatial memories (Teng and Squire, 1999) are not as rich and are lacking in details compared to the remote memories of normal subjects (Rosenbaum et al., 2000). This is also a possibility for the results of another study which seems to support the standard model of memory consolidation in mice (Bontempi et al., 1999). In this study, 2-deoxyglucose uptake was greater in cortical areas than in the hippocampus during the retrieval of remote spatial information (25 days) vs. relatively recent spatial information (5 days). However, the accuracy scores for the mice in the remote condition, although significantly above chance, were significantly lower than that of the mice in the recent condition. The results of these studies are consistent with the present in that they outline the possibility that differential expression of the remote memory for object location in the HPC-REMOTE rats (the preference for the displaced object but not for the NEW or FORMER object-quadrants) was due to the acquisition and retrieval of spatial information by extra-hippocampal brain areas. The impairment observed in the HPC-RECENT rats may reflect the possibility that spatial information in these areas requires sufficient postfamiliarization processing before it can be retrieved.

**Differential Memory Expression in REMOTE and RECENT Conditions**

Why did the expression of spatial memory differ in the SHAM-RECENT and SHAM-REMOTE conditions? It is possible that the delay between the last day of familiarization and the test affected the way in which memories were retrieved. For the rats, a recent memory for the location of an object may be more strongly represented than a relatively more remote memory. This may lead to the differential behavioral expression of recent and more remote memories observed in the present study. Spending more time in the quadrant where an object used to be vs. in the quadrant where an object was displaced to may also reflect the differing amounts of decay associated with recent vs. remote memories. This may not be surprising given the delay between familiarization and testing, which when recovery of the rats is taken into account, is equal to 5 weeks for the rats in the remote condition. However, normal rats have demonstrated intact object recognition memory, in another test that takes advantage of rats’ propensity to explore novelty, after as long or longer retention delays with similar amounts of familiarization used in the present study. For example, in novel-object-preference tests, rats spent more time exploring a novel object over a familiar one they had seen 3 weeks (Mumby et al., 2005), 5 weeks (Gaskin et al., 2003), after familiarization.

It is also possible that when rats are given multiple ways in which to express memory for the spatial configuration of objects relative to allocentric cues, that any one of these ways may be expressed at any given time. In the present case, SHAM-RECENT and SHAM-REMOTE rats expressed their memories by spending more time in the NEW and FORMER quadrants respectively. Lesioned rats only expressed their memory for the previous configuration of the objects by spending more time investigating the displaced object.

That normal rats are not showing preferential object investigation may arise from a form of competition that promotes exploring the global context on the one hand and investigating the source of the change (the displaced object) on the other. Giving more time during the test may have revealed that explorative behavior switches from general context to source (object) for normal rats and source to context for lesioned rats.

One position that can be taken regarding these different behaviors is that they all show that rats remember the previous spatial organization of the objects relative to the spatial cues that surround the arena. In the present study only the rats in the SHAM-RECENT, SHAM-REMOTE and HPC-REMOTE conditions showed evidence of memory through one of the three measures taken. Given an identical test, in which only the familiarization-surgery interval differed, rats in the HPC-REMOTE condition showed evidence that they remembered the previous spatial configuration of the objects, as indicated by investigation ratios that were significantly above chance. In contrast, rats in the HPC-RECENT condition showed no evidence of remembering through any of the measures. Viewed in this way, the results suggest that a hippocampal lesion made within 1–3 days, but not one made 3 weeks after familiarization, resulted in an impairment of allocentric-spatial memory.

It is important to note that if we had not taken the several behavioral measures reported in this study we might have missed the learning that occurred in the SHAM rats, because they did not show a preference for the displaced object but for either one of the NEW and FORMER quadrants. The finding that learning in rats cannot be detected using one measure and detected when using another is not new. Several studies in which this conclusion can be drawn have been reviewed (Wilkie et al., 1999) and the findings of the present study provide further evidence supporting those studies.

Altogether, the findings in the present study suggest that the consolidation of spatial memories may be detected if non-navigational tasks are used. However, care must be taken in the interpretation of these findings as there may be alternative explanations that could potentially eliminate the need to refer to a consolidation process to explain why signs of preserved remote memories were found.

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