

Dissociating the Role of the Parietal Cortex and Dorsal Hippocampus for Spatial Information Processing

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Dorsal hippocampus, parietal cortex, and control lesioned rats were tested on both a metric and topological task. The metric task consisted of 2 different objects placed 68 cm apart on a cheese board. After habituation, the objects were moved to a separation of 38 cm on Day 1 and to a separation of 98 cm on Day 2. The topological task consisted of 4 different objects placed in a square orientation. After habituation, the first 2 objects were switched, and after the rats habituated to that change, the back 2 objects were switched. This was repeated on a different day with 4 new objects. The data suggest that the hippocampus is necessary for metric representations, whereas the parietal cortex is necessary for topological representations.

Keywords: dorsal hippocampus, parietal cortex, metric, topological, novelty

It has been proposed that spatial relationships and spatial information are critically involved in the formation of a spatial cognitive map (O'Keefe, 1990). An important finding is that spatial knowledge assists guided and appropriate navigation through an environment (Long & Kesner, 1996; Poucet, 1993). However, among the various features of spatial representations, there is a need to model the theoretical and neurobiological representations of the cognitive map. It has been proposed that there exists two fundamental and basic features of space—metric and topological relationships between stimuli. These properties of space can also be processed independently. *Metric relationships* are defined as the relationship of angles and distances between objects as well as linear and angular distances, whereas *topological relationships* are represented by a connectedness relationship between objects that cannot be affected by metric modifications (Gallistel, 1990; Herrmann & Poucet, 2001; Kuipers & Levitt, 1988; Poucet, 1993). Topology, more specifically, is based on "... the notions of continuity and limit, from which are derived the relations of compactness, neighborhood, enclosure, and connectivity" (Poucet, 1993, p. 168). Therefore, metric transformations are created by altering distances and angles between objects, whereas topological transformations involve either stretching or contracting the entire environment as a whole or disrupting particular relationships of enclosure or connectivity (Gallistel, 1990).

Previous experiments have shown that the hippocampus (HPC) is responsible for spatial information processing (Buhot, Foreman,

Poucet, & Save, 1992; Cassel, Galani, Kelche, & Weiss, 1998; Long & Kesner, 1996; O'Keefe & Nadel, 1978), as well as the parietal cortex (PC; Buhot et al., 1992; DiMattia & Kesner, 1988a, 1988b; Kesner, Long, & Mellem, 1998; Long & Kesner, 1998a, 1998b). Several models have suggested that the HPC and PC process different features of spatial information. Understanding how the HPC and PC interact during spatial information processing and how each region processes this information separately is important to understanding how spatial information is processed overall for the emergence of a cognitive map. We propose a dissociation in which the dorsal hippocampus (dHPC) is responsible for metric information processing, whereas the PC is responsible for topological information processing.

Animal exploration is crucial to the development of a cognitive spatial map via orthogonalizing information about the surrounding environment (Cassel et al., 1998; Poucet, 1993; Thinus-Blanc, Poucet, & Save, 1998). Because animals (e.g., rats) naturally familiarize themselves with their environment (Poucet, 1993), it is often the case that animals show extensive exploration in a novel environment. Therefore, if the environment is unfamiliar to a rat, then intense exploration will occur until it becomes familiar (*habituation*); but when any change occurs within the environment, increased reexploration will ensue (*dishabituation*; Buhot et al., 1992; Thinus-Blanc et al., 1998). In the current experiments, the level of spatial knowledge was based on these exploratory behaviors. The topological task involved four objects placed in a square configuration on a cheese board, and after habituation, objects were swapped without altering the geometric configuration (see Figure 1A). The metric task involved two different objects 68 cm apart on a cheese board that were moved to a separation of either 38 cm or 98 cm after habituation (see Figure 1B). We hypothesized that lesions of the dHPC would disrupt reexploration on the metric task, whereas lesions to the PC would disrupt reexploration on the topological task when compared with a control group.

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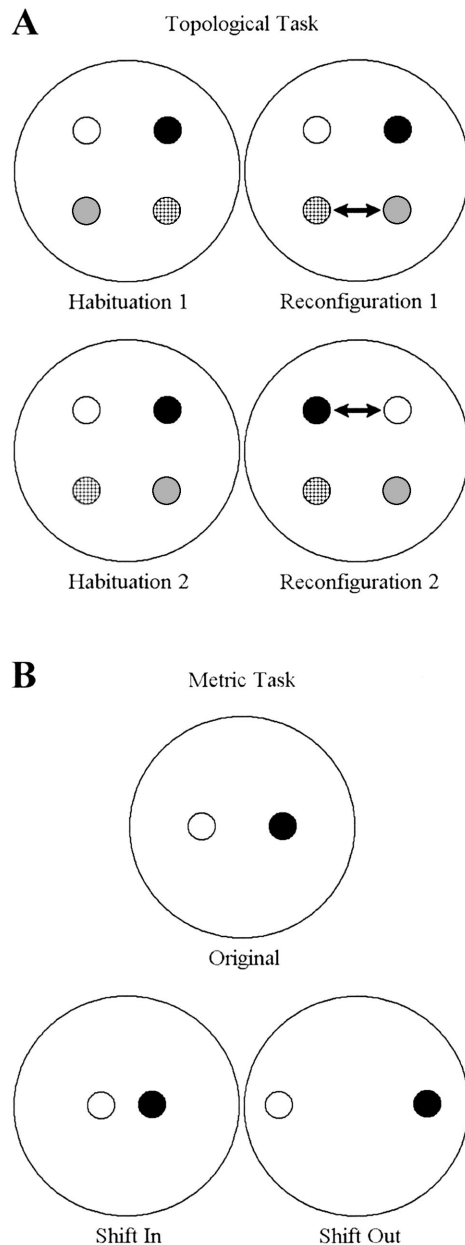


Figure 1. A. Topological task. Displayed are the general object geometric configurations on top of the round board. In the first diagram, rats are habituated to the original geometric configuration. In the second diagram, the front two objects are transposed, creating a topological alteration. In the third diagram, rats are habituated to the new configuration. In the last diagram, the back two objects are transposed, creating another topological alteration. B. Metric task. Displayed are the object positions on top of the round board. In the first diagram, rats habituate to the original metric distance between the objects (i.e., 68 cm apart). In the second diagram, the metric reconfiguration for the first task shortens the distance between the objects to 38 cm apart. In the last diagram, the metric reconfiguration for the second task lengthens the distance between the objects to 98 cm apart.

Method

Subjects

A total of 24 Long-Evans rats (260–400 g) were housed independently in standard plastic rodent cages and maintained on a 12-hr light–dark cycle. All testing was conducted in the light portion of the light–dark cycle. They were free fed and allowed access to water ad libitum. All animal care and experimental procedures conformed to the National Institutes of Health and Institution for Animal Care and Use Committee's guidelines for proper care and use of experimental animals.

Surgery

All rats were handled 15 min daily for 1 week prior to surgery. Rats were randomly assigned to a surgery group (PC, dHPC, control). Rats were anesthetized with isoflurane. Each rat was placed in a stereotaxic apparatus (David Kopf Instruments, Tujunga, California) with an isothermal heating pad to maintain body temperature at 37 °C. With its head level, the scalp was incised and retracted to expose bregma and lambda and positioned them in the same horizontal plane. dHPC lesions were made with ibotenic acid; 20 μ l was injected at 6 μ l/hr with a microinfusion pump bilaterally into three sites within the dHPC (2.8 mm posterior to bregma, 1.6 mm lateral to the midline, 3.0 mm ventral to dura; 3.3 mm posterior to bregma, 1.8 mm lateral to the midline, 2.8 ventral to dura, 4.1 mm posterior to bregma, 2.6 mm lateral to the midline, 2.8 ventral to dura). PC lesions were made via aspiration. The lesions were from 1 mm posterior to bregma to 4.5 mm posterior to bregma, 2 mm lateral to midline to approximately 1 mm above the rhinal sulcus in the medial–lateral plane, and 2 mm ventral to dura. Half of the control rats received dHPC vehicle injections, and the other half received sham surgery. Following surgery, the incisions were sutured, and the rats were allowed to recover for 1 week before experimentation.

Materials and Experimental Procedures

A round board served as the testing apparatus for the experiment. In addition, an orange curtain completely covered the maze. The surface of the apparatus stood 65 cm above the floor, was 119 cm in diameter, and was 3.5 cm in thickness. The apparatus was kept in a well-lit room with no windows; one door, one chair, one small table, and posters on the walls served as spatial cues. A video camera was positioned directly above the maze. All trials were videotaped.

All rats were tested twice on both of the tasks for a total of 4 days of testing: Order of metric and topological tasks was counterbalanced, and different objects were used for each test. Prior to training, rats were randomly assigned to receive dHPC ($n = 6$), PC ($n = 6$), or control sham ($n = 12$) lesions. The dependent variable on all the tasks was exploration time with the objects.

The topological task was based on a novelty detection paradigm of five 5-min sessions, with a 3-min first and third intersession interval and a 10-min intersession interval for the second and fourth intersession interval. For the topological test, four different objects were placed in a square arrangement, which were all 68 cm apart on the cheese board. Sessions 1 and 2 allowed for familiarization and habituation. During Session 3, after the 10-min intersession, the front two objects were transposed. Sessions 3 and 4 allowed for exploration and habituation to the new configuration. During Session 5, the back two objects were switched. For the second topological test, four entirely different objects were used on the same topological paradigm 48 hr later (see Figure 1A). The dependent measure was the difference of reexploration between displaced objects and nondisplaced objects on Session 3 and Session 5.

The metric task was also based on a novelty detection paradigm of four 5-min sessions, with a 3-min first and second intersession interval and a

10-min intersession interval for the third intersession interval. On the first metric test, two different objects were placed 68 cm apart on the cheese board. Sessions 1, 2, and 3 allowed for familiarization and habituation. During Session 4, after the 10-min intersession, the two objects were moved so that the separation was 38 cm apart. For the second metric test, two different objects were used on the same metric paradigm 48 hr later; however, on Session 4, the two objects were moved so that the separation was 98 cm apart (see Figure 1B). The dependent measure was the amount of reexploration during Session 4 as compared with Session 3.

Histology

At the end of the experiments, each rat was given a lethal interperitoneal injection of sodium pentobarbital. The rat was perfused intracardially with 10% (wt/vol) Formalin in 0.1 M phosphate buffer. The brain was then removed and stored in 30% (vol/vol) sucrose–Formalin for 1 week. Transverse sections (24 μ m) were cut with a cryostat through the lesioned area and stained with cresyl violet. A program, ImageJ 1.31 (National Institutes of Health, Bethesda, Maryland), was used to quantify the extent of the lesion.

Results

Histological Analysis

Ibotenic acid was used to produce lesions of the dHPC. Although it is difficult to define the exact boundary that separates the dorsal from the ventral component of the HPC, the *dorsal region* is defined as the anterior 50% of the HPC (Moser & Moser, 1998). A quantitative analysis revealed that a dHPC lesion resulted in 95% damage to the dHPC with less than 5% damage to the ventral HPC and less than 5% damage to the overlying cortex (see Figure 2A). The less than 5% sparing of the dHPC was usually in the subiculum or small remnants of the lower blade of the dentate gyrus. In one case, there was unilateral sparing of CA3 pyramidal cells at the most lateral aspect adjacent to the fimbria, but this accounted for less than 2% of the dHPC; area CA1, the dentate gyrus, and the hilus were ablated. On the basis of microscopic observation of cresyl-violet-stained sections, ibotenic acid lesions produced little damage, if any, in other extrahippocampal areas of the brain, including the entorhinal cortex. Also, it should be noted that on the basis of the use of Fluorograde to examine cell death 2 days following ibotenic acid lesions, there was no observable cell death outside the HPC (Jerman, Kesner, Lee, & Berman, in press).

Aspiration was used to lesion the PC. The lesions extended from 1 mm posterior to bregma to 4.5 mm posterior to bregma, and 2 mm lateral to midline to approximately 1 mm above the rhinal sulcus in the medial-lateral plane (see Figure 2B). There was some sparing of the PC at the ventrolateral aspect adjacent to the temporal association cortex as well as some sparing between 1 and 2 mm lateral to midline, but these sparings accounted for less than 10%. The PC lesions generally did not result in damage to the dorsal or ventral HPC, fimbria–fornix, or temporal cortices. In one case, there was unilateral damage to the lateral aspect of area CA1, but this accounted for less than 10% of area CA1. There was some anatomical deformation of the HPC into the empty space created by removal of the PC, but the HPC remained intact and showed no signs of damage.

Behavioral Analysis

Topological. Figure 3A represents the time course of average grid crossings for each lesion group during the first habituation sessions (Sessions 1 and 2) and indicated that all three groups displayed habituation across sessions, but the PC group showed more grid crossings. There was a significant main effect of the lesion group, $F(2, 30) = 7.33, p < .001$, with significant effect of session, $F(1, 30) = 19.05, p < .0001$, and no significant Lesion \times Session interaction, $F(2, 30) = 1.51, p < .24$. A subsequent Student–Newman–Keuls test for the group effect revealed that the control and dHPC groups did not differ significantly from each other, whereas the control and PC groups did differ significantly ($p < .01$). The PC group was also significantly different ($p < .05$) from the dHPC group. Figure 3B represents the time course of average grid crossings for each lesion group during the second habituation session (Sessions 3 and 4) and indicated that all three groups displayed habituation across sessions, but the PC group again showed more grid crossing. There was a significant main effect of the lesion group, $F(2, 37) = 14.34, p < .0001$, with significant effect of session, $F(1, 37) = 7.24, p < .01$, and no significant Lesion \times Session interaction, $F(2, 37) = 0.51, p < .61$. A subsequent Student–Newman–Keuls test for the group effect revealed that the control and dHPC groups did not differ significantly, whereas the control and PC groups did differ significantly ($p < .01$), as well as the PC and dHPC groups ($p < .01$). Because the PC lesioned group displayed overall heightened activity, we standardized the time (in seconds) of object exploration using the following ratio. The total time spent exploring the displaced objects during the first reconfiguration session (Session 3) was divided by the sum of the total time spent exploring the nondisplaced objects and itself, thereby creating the ratio A divided by the sum of A plus B. This formula was repeated with the second reconfiguration session (Session 5). Table 1 displays the mean exploration times (in seconds; plus or minus the standard error) per displaced and nondisplaced objects for each group for Sessions 3 and 5. It should be noted that for the dHPC rats, there was some variability across tests, in that dHPC rats reexplored for the first, second, and third reconfiguration sessions but did not reexplore for the last reconfiguration session. However, as can be seen in Figure 4A, the average of the four sessions revealed an overall increased reexploration for the dHPC group. Figure 4A shows the average ratio of exploration time of the displaced objects during the reconfiguration session divided by the sum exploration time of the displaced objects and nondisplaced objects of the same session ($0.5 =$ no preference), indicating that the PC lesioned group displayed no reexploration of displaced objects when compared against the nondisplaced objects, whereas the dHPC and control group did reexplore. A one-way analysis of variance using the ratios revealed a significant group effect, $F(2, 21) = 11.30, p < .0005$. A subsequent Student–Newman–Keuls test for the group effect revealed that the control group and dHPC group did not differ significantly from each other, whereas the PC group did differ significantly from control ($p < .01$), as well as from the dHPC group ($p < .05$).

Metric task. Figure 3C represents the time course of average grid crossings for each lesion group during the habituation sessions (Sessions 1–3) and indicated that all three groups displayed habit-

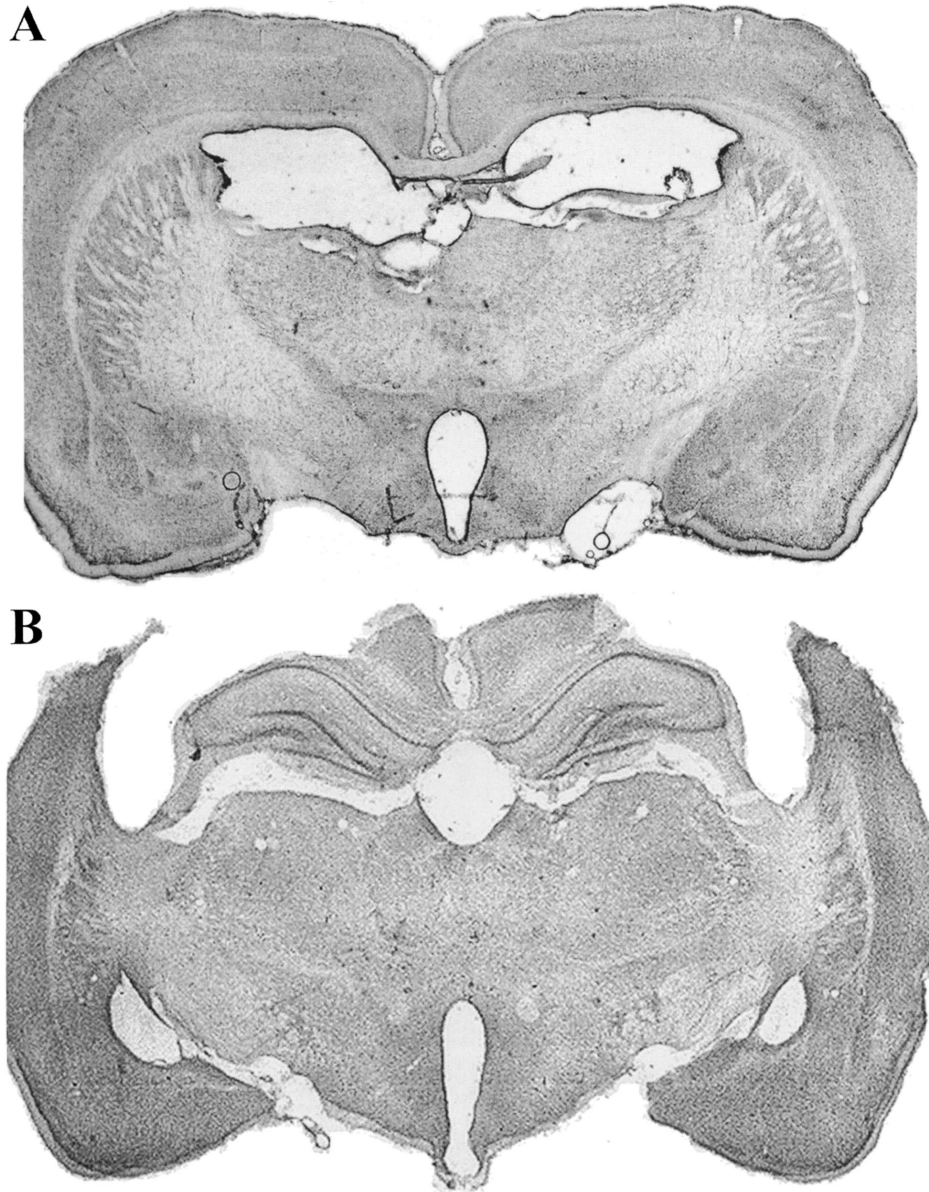


Figure 2. A. Photomicrographs (multiplied by 12.5) of a representative section of a dorsal hippocampus lesioned rat. B. Photomicrographs (multiplied by 12.5) of a representative section of a parietal cortex lesioned rat.

uation across sessions, but the PC group showed more grid crossings. Habituation occurred in all groups and was indicated by a significant main effect of lesion group, $F(2, 41) = 23.58, p < 0.0001$, with significant effect of session, $F(2, 82) = 56.93, p <$

$.0001$, and no significant Lesion \times Session interaction, $F(4, 82) = 1.30, p < .28$. A subsequent Student–Newman–Keuls test for the group effect revealed that the control and dHPC groups did not differ significantly from each other ($p < 0.086$), whereas the

Figure 3 (opposite). A. Topological task. Habituation 1: Graphed is the time course of average grid crossings for each lesion group for Sessions 1 (SS1) and 2 (SS2). B. Topological task. Habituation 2: Graphed is the time course of average grid crossings for each lesion group for Sessions 3 (SS3) and 4 (SS4). C. Metric task. Graphed is the time course of average grid crossings for each lesion group for SS1–SS3. Habituation was observed for all lesion groups for Figures 3A, 3B, and 3C. PC = parietal cortex; dHPC = dorsal hippocampus.

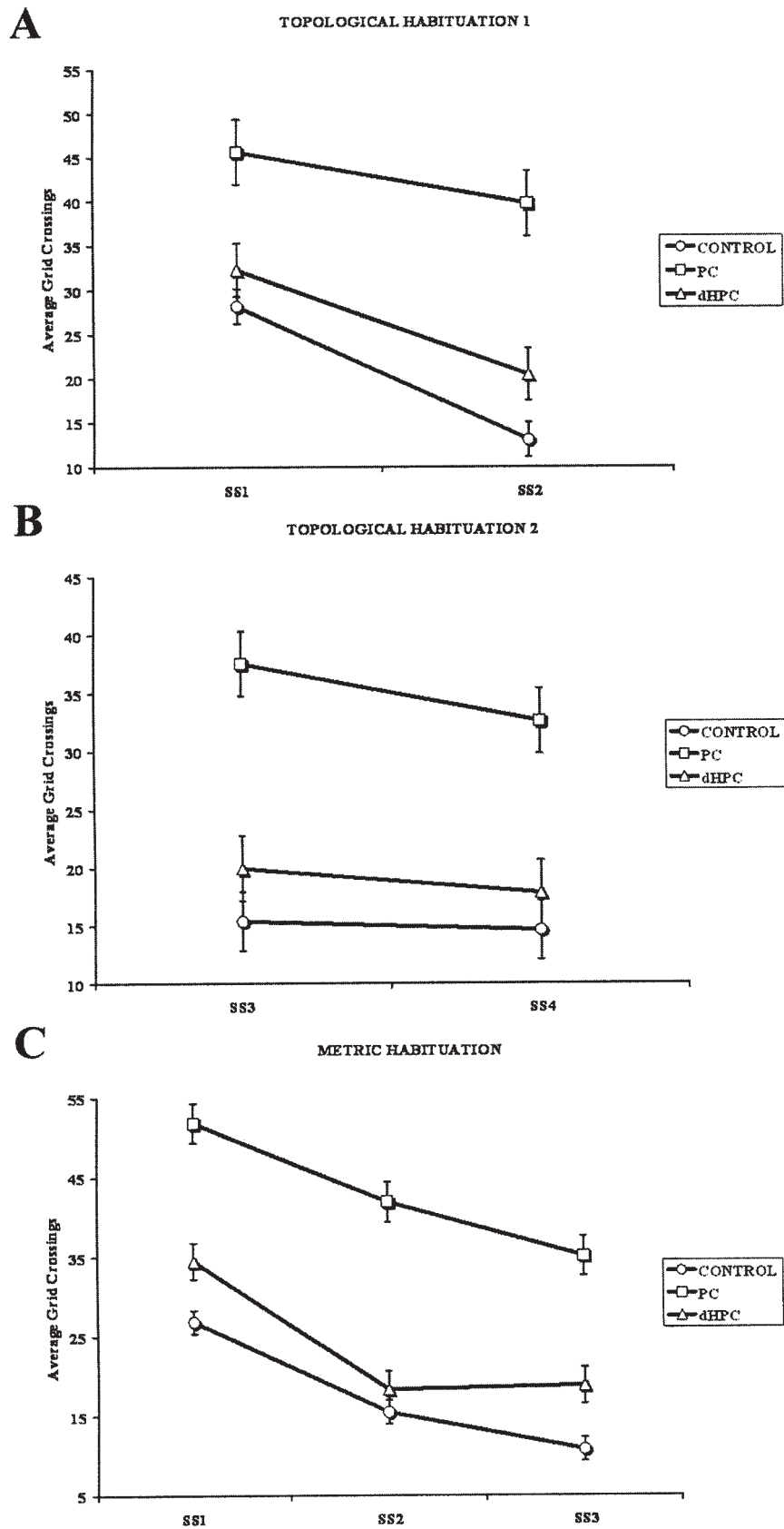


Table 1
Topological Task Mean Exploration Times (in Seconds; Plus or Minus the Standard Error) per Displaced and Nondisplaced Objects for Each Group for Test 1 Sessions 3 and 5 and Test 2 Sessions 3 and 5

Group	<i>n</i>	Session 3		Session 5	
		Nondisplaced	Displaced	Nondisplaced	Displaced
Test 1					
Control lesioned	12	2.10 ± 0.53	3.90 ± 1.16	1.50 ± 0.56	3.00 ± 1.10
PC lesioned	6	5.17 ± 1.01	6.83 ± 0.91	3.17 ± 0.70	1.83 ± 0.65
dHPC lesioned	6	2.00 ± 0.82	5.33 ± 1.61	1.20 ± 0.37	2.20 ± 0.92
Test 2					
Control lesioned	12	1.75 ± 0.09	3.00 ± 1.08	1.50 ± 0.65	5.75 ± 1.03
PC lesioned	6	14.67 ± 3.96	11.17 ± 3.15	4.67 ± 2.03	4.67 ± 1.26
dHPC lesioned	6	2.17 ± 0.60	3.83 ± 1.05	2.50 ± 0.56	1.83 ± 0.79

Note. Sessions 3 and 5 = reconfiguration sessions; nondisplaced objects = the same location; displaced objects = transposed with each other; PC = parietal cortex; dHPC = dorsal hippocampus.

control and PC groups did differ significantly ($p < .01$), as well as the dHPC and PC groups ($p < .01$). Because the PC lesioned group yet again displayed heightened activity, the time (in seconds) of object exploration was standardized by the following different ratio. The total time spent exploring all objects during the reconfiguration session (Session 4) was divided by the addition of the total time exploration of all objects during the previous session (Session 3) and itself (Session 4), thereby creating a ratio of A divided by the sum of A plus B. Table 2 displays the mean exploration times (in seconds; plus or minus the standard error) per nondisplaced objects (Session 3) and displaced objects (Session 4) for each group. Figure 4B represents the ratio of object exploration during the reconfiguration session divided by the sum total of the object exploration during the previous session and reconfiguration session ($0.5 = \text{no preference}$), indicating that the dHPC rats did not reexplore the displaced objects during the reconfiguration in comparison with the same objects in the previous session, whereas the PC and control rats did reexplore. A one-way analysis of variance using the ratios indicated a significance, $F(2, 21) = 7.12$, $p < .005$. A subsequent Student–Newman–Keuls test for the group effect revealed that the PC lesioned group did not differ significantly from the control group, whereas the control group was significantly different from the dHPC lesioned group ($p < .01$).

The dHPC lesioned group did not differ significantly from the PC lesioned group.

Discussion

The results of the current topological task clearly indicate that the PC is essential to processing topological information. The PC lesioned group displayed marked disruption of object reexploration during the topological reorganizations. However, the control and dHPC lesioned groups showed normal habituation and dishabituation behavior and no disruption of object reexploration. The PC lesioned group not only had a deficit on object reexploration but they also displayed continuous habituation instead of increased exploratory behavior during the topological reconfiguration session.

The results are consistent with patient R. M., who had a bilateral PC lesion. This patient demonstrated impairment for learning topological relationships. R. M. was asked to determine whether a large dot was outside or inside a circle. R. M. was unable to learn this task, averaging 49% correct (18 of 37 trials; Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997). Similar observations have shown identical behavioral results with PC lesioned rats (unpublished raw data; Goodrich & Kesner, 2005). Initially, con-

Figure 4 (opposite). A. Topological task. Graphed is an average ratio for Sessions 3 and 5 of reexploration time that the rats spent with the displaced objects during the reconfiguration session divided by the sum time of the displaced objects and nondisplaced objects. Parietal cortex (PC) lesioned rats did not reexplore the displaced objects, whereas the controls and dorsal hippocampus (dHPC) lesioned rats showed preference to the displaced objects ($0.5 = \text{no preference}$). Therefore, the observed dissociation indicates that the PC mediates topological information processing, whereas the dHPC does not. B. Metric task. Graphed is an average ratio of reexploration time that the rats spent with the objects during the reconfiguration session divided by the sum time during the final habituation session and reconfiguration session. dHPC lesioned rats were deficient in object reexploration, whereas the controls and PC lesioned rats showed preference to the displaced objects ($0.5 = \text{no preference}$). Therefore the dHPC mediates metric information processing.

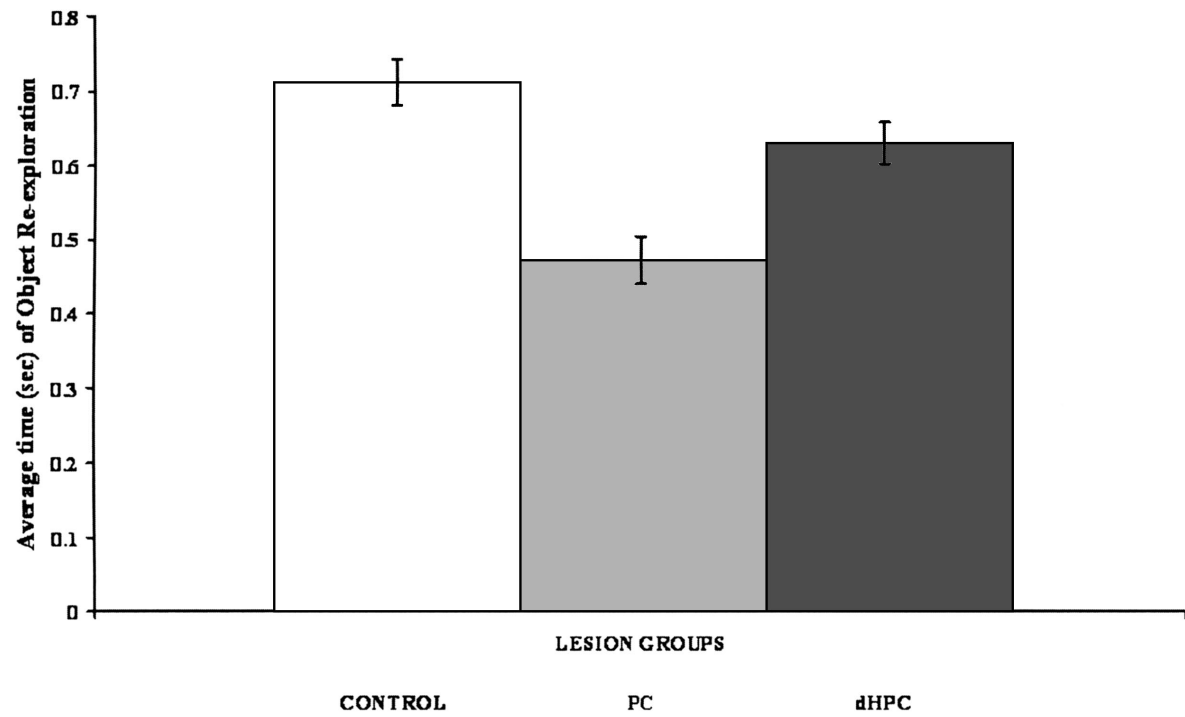
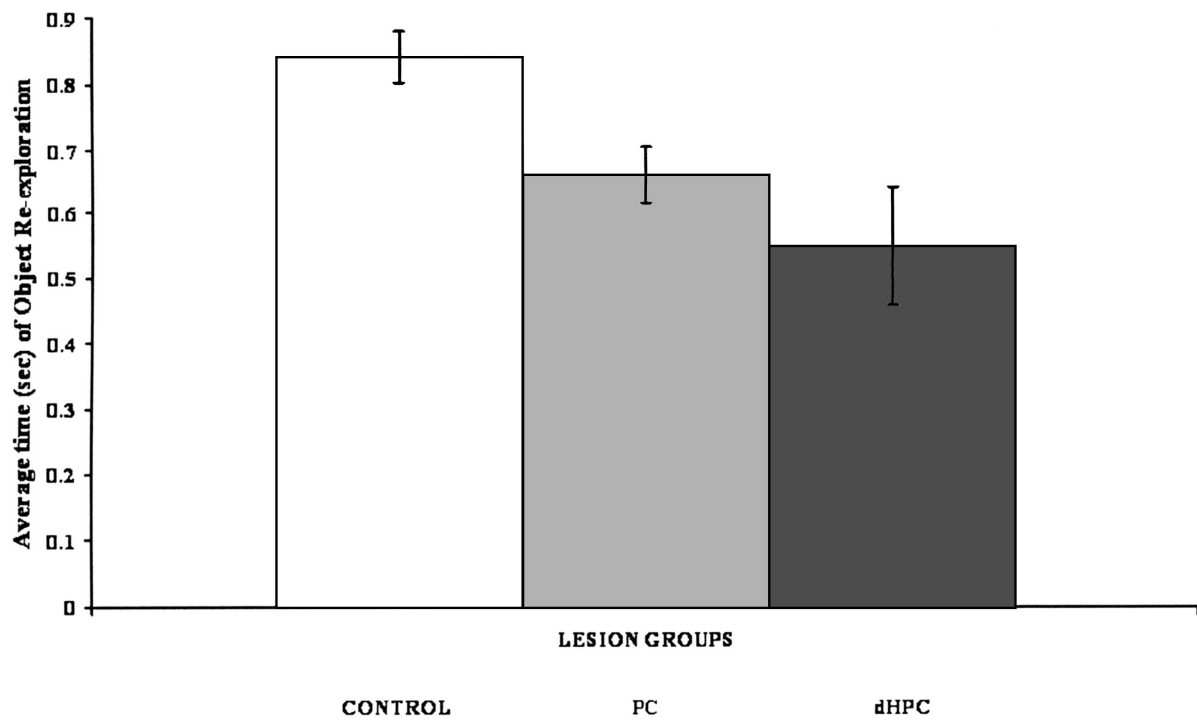
A**TOPOLOGICAL INFORMATION PROCESSING****B****METRIC INFORMATION PROCESSING**

Table 2

Metric Task Mean Exploration Times (in Seconds; Plus or Minus the Standard Error) per Nondisplaced Objects (Session 3) and Displaced Objects (Session 4) for Test 1 and Test 2 for Each Group

Group	<i>n</i>	Session 3 Nondisplaced	Session 4 Displaced
Test 1			
Control lesioned	12	0.30 ± 0.15	2.50 ± 0.52
PC lesioned	6	5.00 ± 1.24	8.67 ± 0.12
dHPC lesioned	6	1.83 ± 0.70	2.17 ± 0.87
Test 2			
Control lesioned	12	1.00 ± 0.42	2.80 ± 0.92
PC lesioned	6	3.33 ± 0.96	8.67 ± 2.40
dHPC lesioned	6	1.33 ± 0.56	2.00 ± 0.78

Note. Session 3 = habituation; Session 4 = reconfiguration; nondisplaced objects = objects to be displaced in Session 4; displaced objects = objects that have been metrically displaced; PC = parietal cortex; dHPC = dorsal hippocampus.

trol rats were trained to discriminate between either a ball inside a ring or outside a ring. After reaching criterion, the rats received PC lesions, and when retested, they were unable to make the discrimination.

Topological spatial information is based on associations between objects that involve relationships such as connectivity and containment (Gallistel, 1990; Herrmann & Poucet, 2001; Kuipers & Levitt, 1998; Poucet, 1993). According to Poucet (1993), "... topology is a geometry originally based on the notions of continuity and limit, from which are derived the relations of compactness, neighborhood, enclosure, and connectivity" (p. 168). Topological information is a crude description of space, because distances and angles have no effect (Gallistel, 1990; Poucet, 1993). On the basis of behavioral experiments, Poucet (1993) and Thinus-Blanc et al. (1998) have demonstrated that topological information, though crude in its representations of space, is essential to rats' spatial representations. Also, because rats encode geometric relationships, they might extrapolate overall geometric structures as well, implying the use of topological information processing. In one experiment, rats were trained to choose arms in a rectangular orientation in the order of their baited magnitudes up to asymptote. Intermittent test trials were administered between the control trials that altered the rectangular formation. During a counterclockwise rotation (i.e., topological shift) of the baited arms, the rats' ability to choose arms on the basis of the bait magnitudes was destroyed (Gallistel, 1990). As a result, topological features of space can be a significant feature to spatial representations.

In the current experiment, the dHPC lesioned group showed marked disruption of object reexploration during the metric tasks, whereas the PC lesioned group displayed no disruption of reexploration. Therefore, the dHPC appears to be crucial for processing metric spatial information, whereas the PC does not process metric information. The control and PC lesioned group displayed normal habituation and dishabituation behavior; their exploratory behavior increased during the metric reconfiguration session. The data also

suggest that dHPC rats contain a normal ability to detect novelty. Although the dHPC rats displayed a deficit on the metric task as predicted, they displayed an overall normal reexploratory behavior on the topological task. Therefore, it is suggested that the dHPC displays impairment for novel metric information and not novelty detection for all types of information.

The results are consistent with the observations of Gilbert and colleagues (DeCoteau, Gilbert, & Kesner, 1998; Gilbert, Kesner, & Lee, 2001), who reported that the dHPC lesioned group showed an inability to distinguish between an object in the correct location and an object in a foil location when under approximately 50 cm, such that lesions of the dHPC disrupted spatial pattern separation. These results suggest that the dHPC is responsible for metric information processing (Kesner, Lee, & Gilbert, 2004).

Metric spatial information is based on associations between objects that involve relationships such as distances and angles (Gallistel, 1990; Herrmann & Poucet, 2001; Kuipers & Levitt, 1988; Poucet, 1993). Specifically, topological information is an unsophisticated concept that only provides a loose representation of space, but when angles and distances are implemented, spatial representations are enhanced (Gallistel, 1990; Poucet, 1993).

It can be argued that an animal's cognitive map is represented by spatial information from an allocentric or absolute frame of reference (independent of one's body position in space; O'Keefe & Nadel, 1978). An alternative view suggests that spatial information can be thought to have both allocentric and egocentric aspects (Gallistel, 1990; Long & Kesner, 1996). Considering an absolute frame of reference, the metric task would also be a topological task because of the objects' connectedness with other distal cues within the environment. Therefore, any shift with an absolute frame of reference would only involve stretching or squishing of the environment, devoid of any metric manipulations. However, the data support the alternative view in that relative to controls, the dHPC disrupts metric, but not topological spatial information and the PC disrupts topological spatial information, but not metric information. Results from previous research have shown that the PC processes egocentric information. For example, patients with right posterior PC lesions are unable to have representations of all parts of space. Edoardo Bisiach found that patients with injury to the right PC could only recall buildings and features on the right side of the Piazza del Duomo square. However, if asked to recall from the opposite side of the square, the patients recalled what was now to their right, which was neglected before because it was to their left (Bisiach & Luzzatti, 1978).

Essentially, we should consider an egocentric perspective for both the metric and topological task. However, if the PC does process egocentric information, then why does the PC lesion group display normal performance on the metric task? Perhaps, metric and topological information are more refined subdivisions of space than of an allocentric and egocentric subdivisions in that they might contribute finer detail about the cognitive map.

The observation that the PC lesion rats had some difficulty with processing metric information could be accounted for by suggesting that there may have been some topological features associated with the metric task in that we used two different objects. Therefore, in addition to detecting a distance change, there might have also been a change in the relationship between these two objects

that may have some topological features associated with it (i.e., connectivity).

In conclusion, the PC displayed significant impairment on the topological task, whereas the dHPC displayed significant impairment on the metric task. Therefore, the current results indicate that the PC is necessary for topological spatial information processing, whereas the dHPC is necessary for metric spatial information processing.

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