ORIGINAL PAPER

Rats build and update topological representations through exploration

Alice Alvernhe · Francesca Sargolini ·
Bruno Poucet

Abstract Although rats are able to build complex spatial representations of their surroundings during exploration, the nature of the encoded information is still a matter for debate. In particular, it is not well established if rats can process the topological structure of the environment in such a way that they are aware of the connections existing between remote places. Here, rats were first exposed for four 5-min trials to a complex environment divided into several sectors that were separated by doors allowing either unrestricted or restricted access to other sectors. In the fifth test trial, we measured the behavior of the animals while they explored the same environment in which, however, they faced changes that either altered or did not alter the topological structure of the environment. In experiment 1, closing previously opened doors prevented the rat from having direct access between corresponding sectors. In experiment 2, opening previously closed doors allowed direct access between sectors that had not been directly accessible. In each experiment, control doors allowed us to discard the mere influence of door manipulation. We compared the rats' exploratory behavior in response to door manipulations that either strongly altered or did not alter the ability to commute between sectors and found evidence that the animals displayed differential reactions to the two types of door manipulations. This implies that during exploration rats build a precise map of the connectivity of space that can be flexibly updated and used for efficient navigation.

Keywords Spatial representation · Exploration · Topology · Rat

A. Alvernhe · F. Sargolini · B. Poucet
Laboratoire de Neurobiologie de la Cognition,
CNRS—Aix-Marseille Université, UMR 6155,
13003 Marseille, France

A. Alvernhe · F. Sargolini · B. Poucet (✉)
Laboratoire de Neurobiologie de la Cognition, Université de
Provence, UMR 6155, Case C, 3 Place Victor Hugo,
13331 Marseille cedex 03, France
e-mail: bruno.poucet@univ-provence.fr

Introduction

It is now widely accepted that some animals, like rats, can form a spatial representation of their environment by gathering spatial information during exploration (Lever et al. 2006; O'Keefe and Nadel 1978). Such spatial information relies not only on the peculiar properties of locations in terms of their individual sensory characteristics, but also on their relationships within space. These relational properties include metric information, i.e., information about angles and distances (Cheng and Spetch 1998; Gallistel 1990) and topological information, which is based on relationships of neighborhood and connectivity (Deutsch 1960; Poucet and Benhamou 1997; Vauclair 1980). Although there is indirect evidence that organisms are sensitive to both types of spatial information, i.e., build both topological and metric representations (Poucet et al. 1986; Thinus-Blanc et al. 1987), few experiments have directly addressed the issue of whether animals can detect purely topological modifications in their environment.

Since exploration is necessary for the acquisition of spatial information, it provides a direct measure of the type of information that is encoded. Such information includes both the intrinsic properties of the environmental items and their spatial relationships. For example, rats react both to a new object introduced in a familiar environment and to a change in the spatial relationships between otherwise familiar

objects by selectively re-exploring the modified items (Save et al. 1992). Therefore, if topological relationships are encoded during exploration, then varying the topological structure of a familiar environment should affect the rats' re-exploration pattern. More specifically, changes that alter topological space should lead to exploratory patterns that differ from those seen after changes that do not greatly alter topological space.

To determine whether rats are able to build a map of the connectivity of currently explored space, we habituated them to a complex environment (a circular arena divided in sectors). Once they were familiar with this environment, the animals were exposed to changes that either strongly altered, or only marginally altered, the topological structure of the arena, i.e., the connectedness between sectors. Our hypothesis was that if topological space is indeed coded by the animals, then strong topological changes should elicit more exploration than changes that only marginally alter the structure of space.

General methods

Subjects

Male Long-Evans rats (R. Janvier, St.-Berthevin, France), weighing 350–450 g and aged 6–8 months, served as subjects. The rats were housed in cages of two animals per cage in a temperature-controlled vivarium (20 ± 2°C) on a natural light cycle and had food and water ad libitum.

Apparatus

In both experiments, the apparatus consisted of a circular arena, 1 m in diameter, in which 30-cm high walls were inserted to create equally sized sectors. When in the arena, the rat could move from one sector to another by traversing small (12 × 10 cm) passageways in the walls. Each wall had two passageways (Fig. 1), which could be open or closed. The floor of the entire arena was covered with wood shavings. A circular curtain, 2 m in diameter, surrounded the arena. A video camera fixed to the ceiling above the apparatus was connected to a video recorder and a monitor located in an adjacent space. The arena was dimly lit by fluorescent lamps. Each sector was equipped with a set of visual cues and a distinctive object so that it was easily and unambiguously identifiable by the animals. Further visual cues were attached to the curtain to facilitate sector discrimination.

Behavioral procedures and analyses

After 10-min daily handling sessions for eight consecutive days, the rats were individually subjected to five consecutive 5-min trials of free exploration of the apparatus: four habituation trials followed by one test trial. On each exploration trial, the rat was introduced in the apparatus in the middle of sector A, facing the associated object (Fig. 1). During the 4-min intertrial intervals, the rat was returned to its home cage and wood shavings on the apparatus floor were shuffled. The four habituation trials were conducted with the apparatus in its standard configuration, whereas the test trial was performed after specific passageways had been opened or closed. To minimize the effect of possible olfactory biases, the experimenter touched all passageways before the test trial.

All trials were filmed and stored on a videodisk and behavioral analyses conducted off-line. Individual paths during each exploration trial (habituation and test) were reconstructed using a video tracker (Viewpoint®). In both experiments, we measured overall locomotor activity and exploration directed at the passageways. Locomotor activity was assessed by measuring the total distance run by the animal during each trial. Runs between sectors were also scored by counting the number of times the rats went through the passageways. Exploration of passageways was quantified by measuring the total time spent by the animal exploring the closure and/or the frame of the passageways. To do so, an exploratory event was counted each time the animal actually touched the passageway with either its snout or its vibrissae. A stopwatch was used to estimate the duration of the contact. Gnawing the frame of the passageways was not counted as an exploratory event as it may stem from a motivation other than exploration directed at the door (e.g., frustration, play, etc.). Similarly, simply staying near the passageway was not scored as exploration. As experimental results were dependent on accurate coding of behavioral events, we assessed scoring reliability in two ways. First, a second rater blind to our hypotheses made an independent assessment of the rats' behavior for trials 4 and 5. The Spearman's rank order coefficient between the scores of the two raters (i.e., the experimenter and the novice rater) yielded an agreement value of $r = 0.91$ ($P < 0.001$). Second, a test–retest reliability index was calculated by correlating the scores obtained by the experimenter across two independent measurements separated by several months. Here again, the Spearman's rank order coefficient between the two measurements was very high ($r = 0.96$, $P < 0.001$), thereby indicating very high scoring reliability.

Experiment 1

In this experiment, we attempted to ascertain whether rats display a stronger exploratory response to the closing of a passageway that prevents access to the adjacent sector than
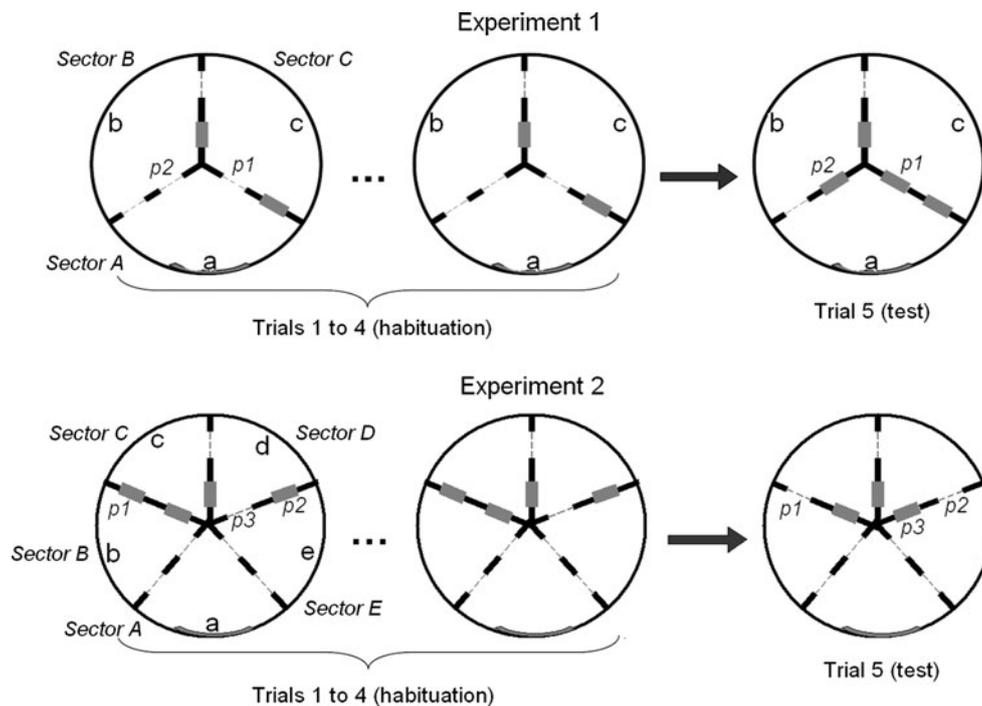
Fig. 1 Apparatus and procedure. The circular arena was divided in sectors separated by passageways shown as *bold gray lines* when closed and as *thin dashed lines* when open. Passageways modified before the test trial are referred to by numbers (*p1*, *p2*, …). *Top* Experiment 1: the arena was divided in three sectors. While passageways *p1* and *p2* were open during habituation trials 1–4, the addition of doors before trial 5 (test trial) blocked the passageways. Closing passageway *p1* induced a strong topological change (i.e., it blocked the access between sectors A and C), whereas closing passageway *p2* induced a moderate topological change (i.e., it did not block the access between sectors A and B). *Bottom* Experiment 2: the arena was divided in 5 sectors. Passageways *p1* and *p2* were closed during habituation trials 1–4, whereas passageway *p3* was open. Before trial 5 (test trial), passageways *p1* and *p2* were opened, whereas passageway *p3* was closed. Opening passageway *p1* induced a strong topological change (i.e., it opened the access between sectors B and C), whereas accessibility between sectors D and E was unaffected by the permutation of open and closed doors at passageways *p2* and *p3*

to a similar change that leaves access to the adjacent sector available.

Methods

Three walls inserted in the cylinder arena delimited three sectors (A, B and C; Fig. 1, top). The four habituation trials were conducted with the apparatus in its standard configuration. In this configuration, four of the six passageways (among which *p1* and *p2*; Fig. 1, top) were open, while the remaining two passageways were closed (Trials 1–4). During the test (trial 5), two of the previously open passageways, *p1* and *p2*, were closed (Fig. 1, top). Even though the closure of these two passageways was equivalent in terms of sensory change, their topological consequences were dramatically different. Closing the test passageway *p1* induced a *strong topological change* since it precluded direct commuting between sectors A and C. In contrast, closing the control passageway *p2* induced a *moderate topological change* since it did not preclude commuting between sectors A and B, which was still possible by using the adjacent passageway. This latter change may therefore be used as a control to assess the impact of topological changes on animals' behavior. To quantify the changes in exploration across trials, we measured locomotor activity, accumulated exploration times directed toward each passageway (and/or frames of passageway), and the total number of runs through each open passageway for each exploration trial.

Results

Habituation (trials 1–4)

Eight rats were tested in this experiment. Habituation during trials 1–4 is shown in Fig. 2a. Both locomotor activity and passageway exploration significantly decreased from trial 1 to trial 4 (repeated-measure ANOVAs, $F_{(3,21)} = 7.30$; $P = 0.0015$ and $F_{(3,21)} = 4.43$; $P = 0.0146$, respectively) such that very little exploration was observed by the last habituation trial. In addition, a repeated-measure ANOVA shows that animals explored open and closed passageways to the same extent ($F_{(1,14)} = 3.17$; $P = 0.096$, Fig. 2a). Finally, passageways *p1* and *p2* were similarly explored

during trial 4 (one-way ANOVA, $F_{(1,14)} = 0.59$, $P = 0.455$, Fig. 2b).

Test trial (trial 5)

Closing the passageway during the test trial induced both a strong increase in locomotor activity relative to trial 4 (repeated-measure ANOVA, $F_{(1,7)} = 24.3$; $P = 0.0017$; Fig. 2a) and a selective exploratory response to the newly closed passageways $p1$ and $p2$ (repeated-measure ANOVA, $F_{(2,21)} = 26.1$; $P < 0.001$; Newman–Keuls, $P < 0.01$ and $P < 0.001$, respectively, for passageways $p1$ and $p2$; Fig. 2b). A one-way ANOVA revealed that exploration of each of the two modified passageways $p1$ and $p2$ was greater than the average exploration of all non-modified passageways during the test trial ($F_{(2,21)} = 25.7$; $P < 0.001$; Newman–Keuls, $P < 0.001$ and $P < 0.001$, respectively, for passageways $p1$ and $p2$). Moreover, whereas passageways $p1$ and $p2$ were similarly explored during trial 4 (cf. above), during the test trial, passageway $p1$ (strong topological change) was significantly more explored than passageway $p2$ (minor topological change) (Newman–Keuls, $P < 0.001$). Consequently, the renewal of exploration from the last habituation trial to the test trial was greater for passageway $p1$ than for passageway $p2$ (one-way ANOVA, $F_{(1,14)} = 10.76$; $P = 0.0055$).

Because passageway $p1$ was closed during the test trial, there was no possibility for animals to commute directly between sectors A and C. In contrast, rats could commute indirectly between A and C by running through sector B, which lay in between. We found that compared to the last habituation trial, in the test trial rats considerably increased their tendency to run between A and C without stopping in B (number of such runs, trial 4: 1.00 ± 0.42, test trial: 3.38 ± 0.82; paired t test, $t_{(7)} = -2.89$; $P = 0.02$). The number of indirect runs between A and C during the test trial became even greater than the total number of indirect runs (i.e., between any two sectors) observed during trial 4 (1.38 ± 0.32, $t_{(7)} = 2.37$; $P = 0.0496$).

Representative paths for trials 1 and 4 (first and last exposure to standard configuration) and for the test trial (exposure to modified configuration) are shown in Fig. 3. The top row of Fig. 3 depicts paths from the rat that was the least active over the entire experiment, whereas the bottom row depicts paths from the most active rat. In spite of obvious differences in the amount of movement across the three sectors, both rats display a qualitatively similar behavioral pattern. During trial 1, paths were complex and covered the entire surface of the apparatus. In trial 4, paths were also meandering but were often restricted to specific places. Finally, closing passageways $p1$ and $p2$ during the test trial induced a renewal of movements across sectors, with an increase in direct paths through sector B (thus allowing the rats to commute between sectors A and C). More activity was observed at passageway $p2$ than at the immediately adjacent passageway, an observation that was statistically confirmed (one-way ANOVA, $F_{(1,14)} = 70.00$; $P < 0.001$). This general pattern was common to all rats
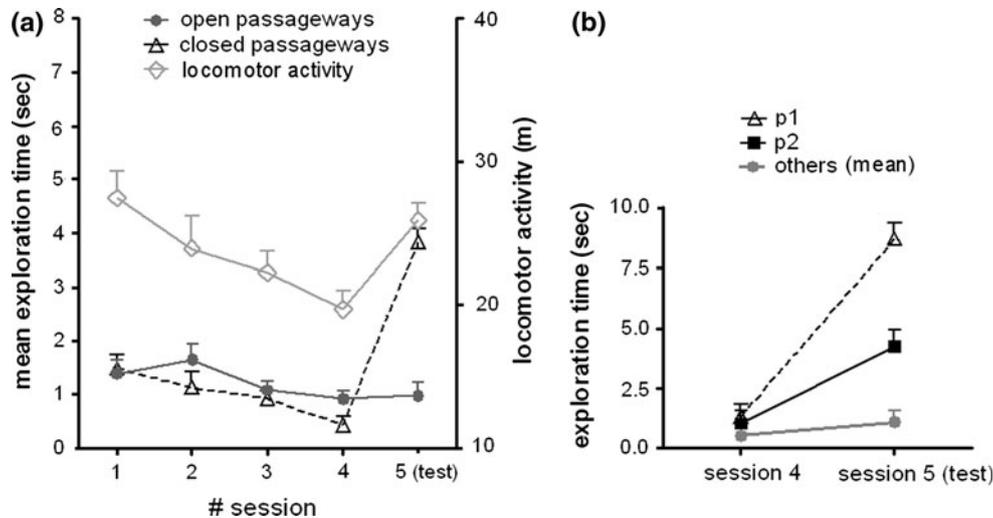

Fig. 2 Behavioral results (Exp. 1). *Left* **a** mean exploration time and locomotor activity across the five trials of the experiment. For each trial, exploration times (in seconds) are averaged per rat and per passageway of each type (i.e., open or closed). All passageways are included in the graph. Locomotor activity is given as the mean distance run per rat for each trial (in meters). Rats displayed a strong exploratory reaction to the change brought to the apparatus during trial 5 and selectively re-explored closed passageways. *Right* **b** mean exploration time of the two manipulated passageways (test: $p1$; control: $p2$) and of all other non-manipulated passageways (*others*) whether they were closed or open. Rats re-explored passageway $p1$ that blocked access between sectors A and C to a much greater extent than passageway $p2$ that did not change the overall connectivity between sectors A and B

and tentatively suggests that re-exploration was focused on the modified passageway and not a non-specific expression of frustration.

Discussion

The results provide clear evidence that rats detected the changes in the environment during the test trial. Furthermore, rats displayed a selective exploratory reaction to the closing of passageway *p1*, which altered the ability to move between sectors A and C, and accordingly modified their exploratory patterns in response to this topological change. Although these findings suggest topological coding, other interpretations are possible. For example, if rats were just looking for an exit to commute between sectors, they would find an alternative exit in the case of *p2* (connection between sectors A and B was preserved via the open passageway adjacent to *p2*), but would persist in their search at *p1*, since there was no direct connection between A and C. Although such behavioral persistence at *p2* cannot be completely ruled out as an explanation, it is not detrimental to the topological coding interpretation. First, the fact that rats tried to reach previously accessible sectors reflects, to some extent, their memory that the former spatial structure allowed such commuting. To cope with the new structure, they relied on a new solution by increasing indirect runs between A and C during the test trial, i.e., rats found an alternative strategy to commute

efficiently between sectors. Presumably, the representation of different routes is by essence topological. Furthermore, passageway *p1* was much more explored than the adjacent, permanently closed passageway, meaning that the rat remembered that only *p1* connected sectors A and C during habituation trials. Such a focused response is hardly compatible with a non-specific persistent behavior caused by frustration and seems to reflect some form of topological coding.

Experiment 2

In the first experiment, we showed that rats specifically reacted to the obstruction of a particular path in an otherwise familiar environment. Although this result is compatible with our topological coding hypothesis, another interpretation in terms of persistent behavior is possible. The aim of Experiment 2 was twofold. First, the demonstration of topological coding required discarding the alternative interpretation of behavioral persistence as described for the first experiment. Second, if rats use a topological representation to navigate more efficiently in current space, they should be able to update this representation when new paths become available. Experiment 2 aimed at testing whether animals would modify their exploratory pattern when facing the appearance of a new shortcut path after the removal of an obstacle in a famil-

Fig. 3 Representative paths (Exp. 1). Paths by the least active (*top*) and most active (*bottom*) rats are shown for trials 1 and 4 (first and last exposure to standard configuration) and for the test trial (exposure to modified configuration). The three sectors are referred to by letters A, B, C (see text for details)
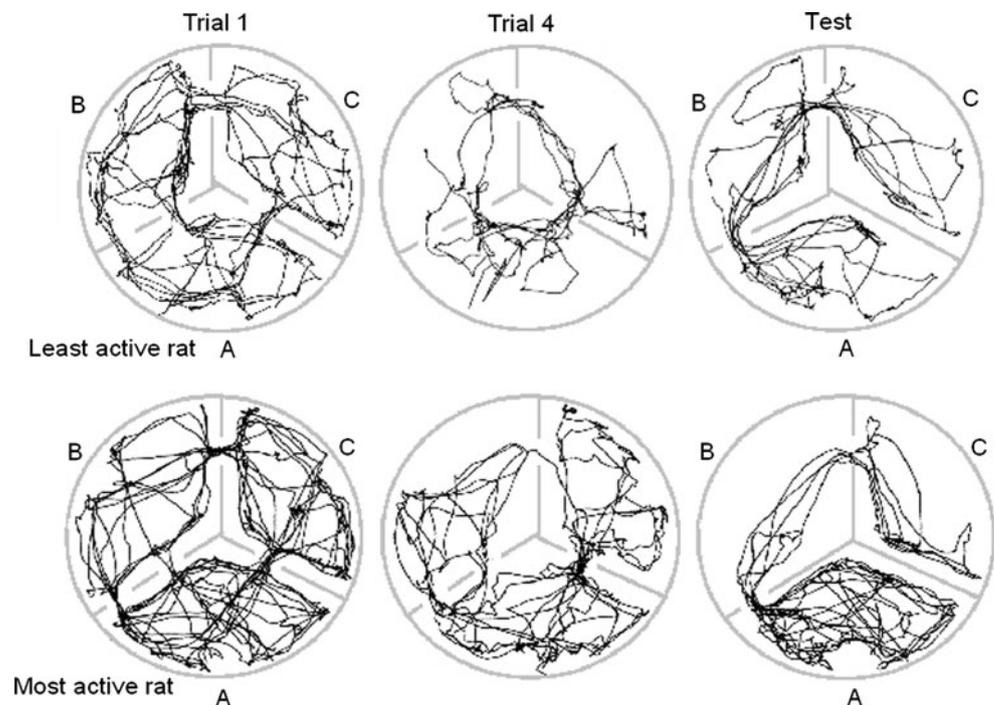
iar environment. The experiment did not involve the blocking of previously available paths between sectors and therefore did not suffer from the caveats of the first experiment.

Methods

The arena was divided into five sectors (A, B, C, D, and E: Fig. 1, bottom). During the first four habituation trials, the rats were exposed to the apparatus in its standard configuration. In this configuration, at least one passageway was open between any two adjacent sectors except between sectors B and C, where two passageways located in the same wall were closed and therefore prevented direct access. In contrast, all other walls had at least one open door, thus allowing the rats to commute directly between adjacent sectors. On the fifth trial (test), passageways *p1* and *p2* were opened and passageway *p3* was closed, and rats were exposed to the novel configuration of the apparatus for 5 min (Fig. 1, bottom). Opening passageway *p1* (*test*) created a direct shortcut between the two adjacent sectors B and C (that, so far, were not directly connected) and was thus topologically more relevant than opening passageway *p2* (*control*). In addition, the consequence of closing passageway *p3* during the test trial was that both sectors B–C and sectors D–E were connected to each other via the most peripheral passageway only, thus facilitating comparison of exploratory responses to *p1* and *p2*. In this regard, it should be noted that opening the control passageway (*p2*) during the test trial did not markedly alter the connection between sectors D and E, since a connection was already available through passageway *p3* during habituation trials. This allowed us to disentangle reaction to topological novelty from non-specific change-induced behavioral effects by comparing two newly opened passageways (*p1* and *p2*), with only one of them (*p1*) strongly altering the spatial topology.

Exploration was analyzed off-line as in Experiment 1. In addition, for the test trial, we sorted the paths that rats performed across the sectors in three different categories, based on the first stopping place after running through open passageways. A stopping place could be the first object, the first passageway, or the first wall explored by the rat after traversing a passageway. We distinguished three types of paths: (1) "local paths": the rat stopped at the passageway that was just run through, or returned to its departure sector, (2) "short paths": the rat stopped in the sector immediately adjacent to the departure sector at a place other than the passageway itself, and (3) "long paths": the rat traversed the sector just accessed (immediately adjacent to the departure sector) to stop in a sector further ahead.

Results

Habituation (trials 1–4)

Ten naïve rats were used for this experiment. Habituation during the first four trials is shown in Fig. 4a. Repeated-measure ANOVAs revealed a significant decrease in both locomotor activity ($F_{(3,27)} = 10.75$; $P < 0.001$) and exploration of the closed passageways ($F_{(3,27)} = 11.85$; $P < 0.001$). In contrast, exploration of open passageways remained relatively stable across trials ($F_{(3,27)} = 0.11$; $P = 0.95$), such that, by the last habituation trial, they became more explored than closed passageways (Newman–Keuls test, $P < 0.05$). Focusing on the three passageways manipulated for the test trial, the consequence was that, during trial 4, passageway *p3* was more explored than passageways *p1* and *p2*, whereas the latter two passageways were explored to the same extent ($F_{(2,27)} = 7.42$, $P = 0.0027$; Newman–Keuls tests, *p3* vs. *p1*: $PP < 0.01$; *p3* vs. *p2*: $P < 0.01$; *p2* vs. *p1*: ns).

Test (trial 5)

Changing the configuration of the apparatus on the test trial induced a significant increase in locomotor activity (repeated-measure ANOVA, $F_{(1,9)} = 53.1$; $P < 0.001$; Fig. 4a) and passageways exploration (repeated-measure ANOVA, $F_{(1,36)} = 110.9$; $P < 0.001$, Fig. 4a). Furthermore, the modified passageways (newly open *p1* and *p2*, as well as newly closed *p3*) were explored to a greater extent than unmodified passageways during the test ($F_{(3,36)} = 14.2$; $P < 0.001$; Newman–Keuls tests, all $P < 0.001$). However, exploration was comparable for all three modified passageways (Newman–Keuls tests, all $P > 0.05$; Fig. 4b).

Although rats went through the newly open passageways *p1* and *p2* equally often (7.0 ± 1.1 vs. 6.9 ± 0.7 times, $t_{(9)} = 0.065$, $P = 0.95$), further analyses revealed different distributions of path types (see methods). While the proportion of short paths was similar and predominant for both passageways (Fig. 4c), local paths were mostly observed at passageway *p1*, whereas long paths were mostly observed at passageway *p2*. This difference was statistically confirmed by a 2-way ANOVA, which revealed significant effects of path type ($F_{(2,54)} = 43.5$; $P < 0.001$) and a significant passageway × path type interaction ($F_{(2,54)} = 12.7$; $P < 0.001$). Newman–Keuls post hoc analyses confirmed the preferential use of local paths for passageway *p1* compared to passageway *p2* ($P < 0.01$) and the preferential use of long paths for passageway *p2* compared to passageway *p1* ($P < 0.01$).

Representative paths for trials 1 and 4 (first and last exposure to standard configuration) and for the test trial (exposure to modified configuration) are shown in Fig. 5
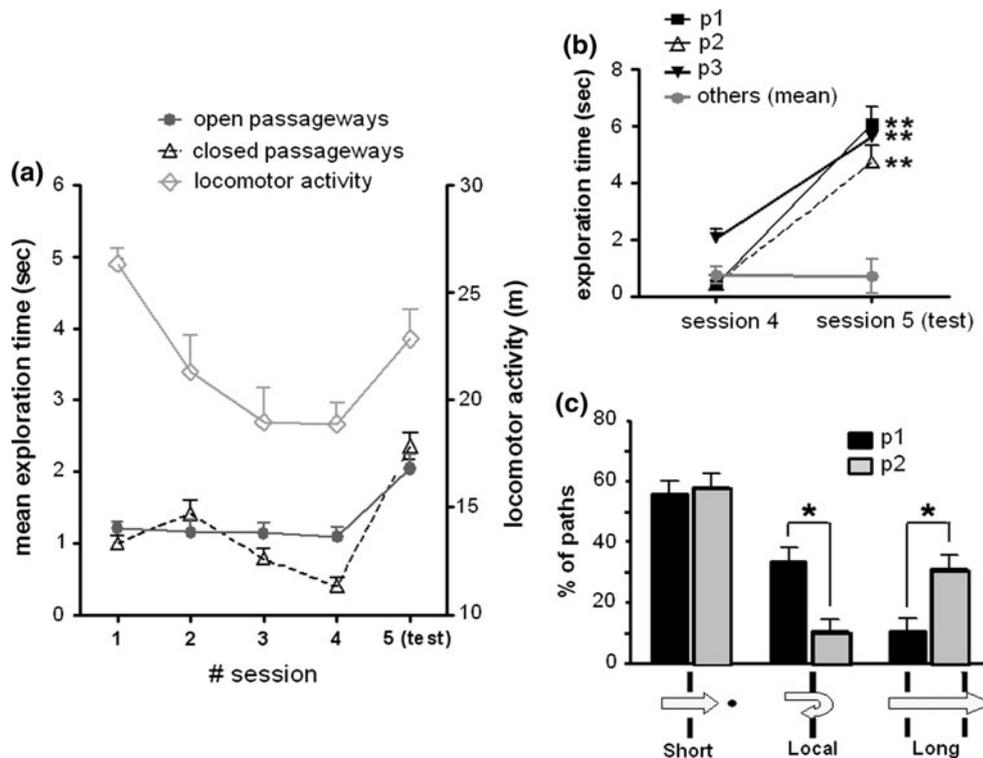
Fig. 4 Behavioral results (Exp. 2). *Left* **a** mean exploration time and locomotor activity across the five trials of the experiment. For each trial, exploration times (in seconds) are averaged per rat and per passageway of each type (i.e., open or closed). All passageways are included in the graph. Locomotor activity is given as the mean distance run per rat for each trial (in meters). Rats displayed a strong exploratory reaction to the change in the apparatus during trial 5, which was greater for open passageways than for closed passageways. *Right* **b** mean exploration time of the three manipulated passageways *p1*, *p2*, and *p3*. All three passageways were re-explored during trial 5. **c** Distribution of path types. Local paths (in which the rat repeatedly crossed the passageway) were mostly observed at passageway *p1*, whereas long paths (in which the rat crossed the passageway to reach a distant sector) were mostly observed at passageway *p2*

for the least active rat (top) and for the most active rat (bottom). As for experiment 1, obvious similarities between the rats' paths can be noticed. During trial 1, paths covered the entire surface of the apparatus, whereas they were restricted to specific places during trial 4. Opening passageways *p1* and *p2* during the test trial induced a clear renewal of movements across sectors, with a majority of local paths at *p1* and long paths at *p2*. On top of this common pattern, a clear preference for inner over more peripheral passageways is noticeable for the south sectors where both types of passageways were available. This observation suggests that commuting between the different portions of the arena was the main motivation for moving through the passageways since using inner passageways shortens the distance from one sector to another.

Discussion

In this experiment, we opened previously blocked passageways so as to determine whether rats would detect and react to the change in the structure of the environment. The design also allowed us to alleviate the drawbacks of

Experiment 1 in terms of persistent behavior. The results showed that rats detected the changes brought to the environment during the test trial and modified their exploratory patterns accordingly. Their reaction was selective for the passageways that had been manipulated, though in a way that differed from Experiment 1. Thus, exploration times towards passageway *p1* and *p2* (the topologically relevant and non-relevant altered passageways) were comparable in Experiment 2, but the rats' strategy in using the two passageways was clearly different. Passageway *p1* was more often associated with local paths (in which rats either stopped or returned to the sector that they just had left) than passageway *p2*. This strategy makes sense since it presumably allowed the rat to encode the newly available connection between sectors B and C as a result of passageway *p1* opening; in contrast, opening passageway *p2* did not alter the connection between sectors D and E since commuting between these two locations was already permitted in previous trials (through passageway *p3*). Our findings therefore demonstrate differential processing of passageways *p1* and *p2*, which differed from each other essentially by the topological change induced by

Fig. 5 Representative paths (Exp. 2). Paths by the least active (*top*) and most active (*bottom*) rats are shown for trials 1 and 4 (first and last exposure to standard configuration) and for the test trial (exposure to modified configuration). The five sectors are referred to by letters A, B, C, D, and E (see text for details)

Representative paths in Experiment 2
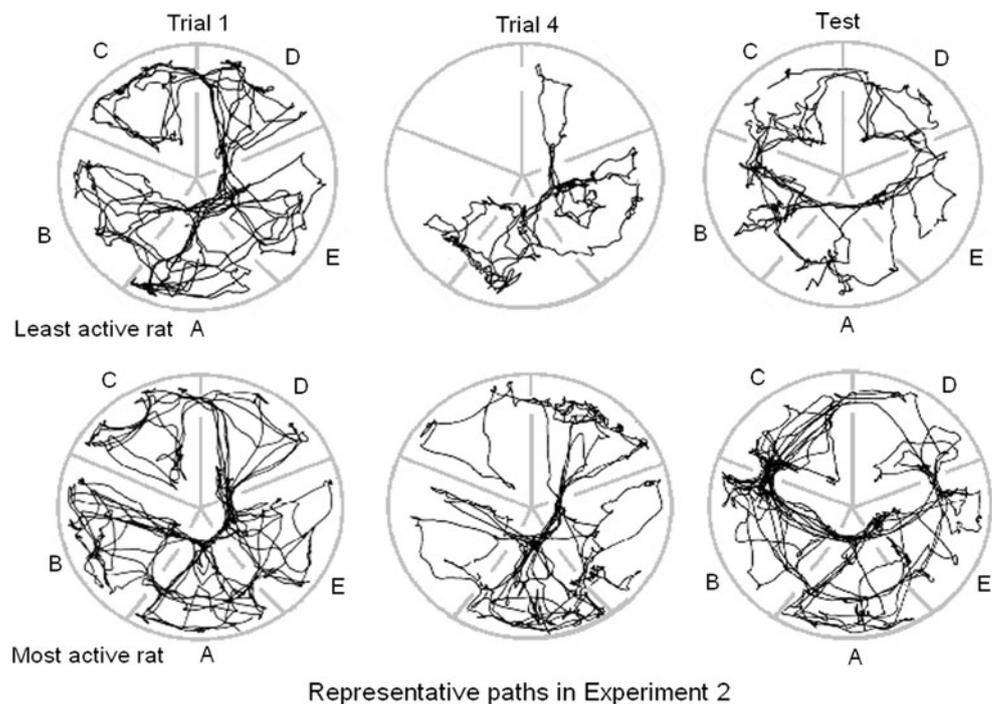
their opening. Although the meaning of the observed differential strategy is speculative, it is consistent with our hypothesis since encoding new paths would rather rely on active movements between places (i.e., local paths) than on static exploration. Although local paths at *p1* may also reflect the detection by the rat of an unexpected event during the test (e.g., sector B can now be accessed from sector C), we argue that such detection necessarily relies on the rat's memory that these sectors were previously not connected. In our view, this memory is topological by essence since it entails connectedness that allows predicting which places are close to each other and therefore may be the basis for sequential coding.

General discussion

In this study, our aim was to determine whether rats would appropriately react to changes that alter the connectivity between places in a familiar environment. In two experiments, rats were accustomed to a circular arena divided in several sectors, over four successive familiarization trials. Following habituation to the initial configuration of the arena, a test trial was conducted in which manipulations of doors at passageways were made either to prevent successful commuting between two adjacent sectors (Experiment 1) or, on the contrary, to allow commuting between two sectors that could not be accessed from each other in the previous trials (Experiment 2). In both experiments, rats were able to detect the changes brought to the initial

structure of the environment and to discriminate the modified passageways on the basis of their topological relevance. Indeed, in Experiment 1, rats re-explored the newly closed passageway that prevented access to the adjacent sector to a much greater extent than a control passageway, whose closing did not prevent the rat to access the adjacent sector. In Experiment 2, door manipulation resulted in similar amounts of exploration at the two newly open passageways. However, rats displayed a specific behavioral strategy for commuting between newly connected sectors, which presumably reflected differential processing of the newly available connection.

Taken together, these experiments suggest that rats encode the topological structure of the environment during exploration. Topological information refers to the relational properties of space such as neighborhood and connectivity and provides a schematic, but operational, representation of space to get acquainted with the structure of the environment (Poucet 1993; Poucet and Benhamou 1997; Schmajuk and Thieme 1992; Schmajuk et al. 1993; Trullier and Meyer 2000). Therefore, topological coding is complementary to other types of spatial coding based on geometry and boundary information or on landmark configurations (see Burgess 2006; Cheng 2008; Lew 2011 for reviews), by providing a way to move between portions of space that do not have stimulus elements in common (Poucet 1993). It is very likely that, under everyday circumstances, topological and metric representations are combined so that the subject is aware both of its location in current space and of the relationship between current and

remote space. For example, in our study knowing which sectors were connected to each other necessarily relied on accurate sector identification, which very likely required taking into account sector-specific landmarks. In addition, both types of coding are useful to maintain up-to-date representations of the environment because, by definition, topological information is not affected by metric distortions. It may therefore be necessary to use topological information when metric representation (i.e., information about angles and distances) is out of register with the actual environment.

Previous evidence for topological coding was provided by experiments on behavior in response to spatial changes, which suggested exploration to be renewed after topological changes (e.g., Poucet et al. 1986), and by path choice studies (e.g., Poucet 1984; Poucet and Herrmann 2001; Poucet et al. 1990). However, these previous experiments suffered from a lack of appropriate control measures. In the present study, this weakness was alleviated by using a protocol in which behavior was measured both at a test location (where the change strongly altered topological structure of the environment) and at a control location (where the same change mildly altered the topology). Comparison of behavior at these two locations revealed that they were well discriminated, implying that rats, in addition to noticing the change, were indeed coding topological relevance.

The implications of such topological coding can be discussed along two different lines. First, several models have considered the role of the hippocampus in the processing of topological information (e.g., Muller et al. 1996). Although the present study supports the notion that topology is indeed encoded, it does not address the role of the hippocampus. Nevertheless, recent evidence from our laboratory has shown that the firing of place cells is strongly altered by modifications of the structure of the environment explored by the animal (Alvernhe et al. 2008, 2011). Although this finding supports the functional implication of the hippocampus in topology encoding, it is based on correlation analyses and therefore does not show a causal relationship between hippocampal activity and topological encoding. A natural experiment to solve this issue would be to assess the behavioral effects of hippocampal lesions in the very simple experimental task described in the present study so as to determine whether rats' differential response to topologically relevant and non-relevant changes is affected by the lesion.

On a different ground, while topological coding in the present study applies to spatial processing, it has implications beyond the domain of space in that it may imply coding of more general relations between events. For example, Eichenbaum (2001) suggests that specific events are associated with specific spatial locations and temporal

tags and that rats are able to link contiguous events through these associated spatial and temporal features. Individual events are embedded in sequences that are encoded in a way that allows the organism both to retrieve the constitutive elements and to predict future events on the basis of their relationships with other events within learned sequences. By essence, the coding of sequential relationships is topological since temporal and spatial contiguity are central to its efficiency. Our study demonstrates that the rat's brain contains the necessary equipment not only to process such relationships, but more importantly, to update them flexibly. Exploration tasks such as the one used in our experiments may therefore be a useful tool for addressing the central issue of how such updating is implemented in the brain.

Finally the present work is in line with studies in artificial intelligence, which stress that, for robot navigation to be efficient, both the global (Euclidean) geometry of space (based on environmental boundaries), and its topology (based on available connections between distinct areas) are encoded (e.g., Yeap and Jefferies 1999). Our results support this general model and show additionally that flexible updating of the topological representation in rats relies on behavioral responses that are selective to the significant changes in spatial connectivity.

References

Alvernhe A, Van Cauter T, Save E, Poucet B (2008) Different CA1 and CA3 representations of novel routes in a shortcut situation. J Neurosci 28:7324–7333

Alvernhe A, Save E, Poucet B (2011) Local remapping of place cell firing in the Tolman detour task. Eur J Neurosci 33:1696–1705

Burgess N (2006) Spatial memory: how egocentric and allocentric combine. Trends Cogn Sci 10:551–557

Cheng K (2008) Whither geometry? Troubles of the geometric module. Trends Cogn Sci 12:355–361

Cheng K, Spetch ML (1998) Mechanisms of landmark use in mammals and birds. In: Healy S (ed) Spatial representation in animals. Oxford University Press, Oxford, pp 1–17

Deutsch JA (1960) The structural basis of behavior. University of Chicago Press, Chicago

Eichenbaum H (2001) The hippocampus and declarative memory: cognitive mechanisms and neural codes. Behav Brain Res 127:199–207

Gallistel CR (1990) The organization of learning. MIT Press, Cambridge

Lever C, Burton S, O'Keefe J (2006) Rearing on hind legs, environmental novelty, and the hippocampal formation. Rev Neurosci 17:111–133

Lew AR (2011) Looking beyond the boundaries: time to put landmarks back on the cognitive map? Psychol Bull 137:484–507

Muller RU, Stead M, Pach J (1996) The hippocampus as a cognitive graph. J Gen Physiol 107:663–694

O'Keefe J, Nadel L (1978) Hippocampus as a cognitive map. Clarendon, Oxford

Poucet B (1984) Evaluation of connectedness by cats in path-selection problems. Percept Mot Skills 58:51–54

Poucet B (1993) Spatial cognitive maps in animals: new hypotheses on their structure and neural mechanisms. Psychol Rev 100:163–182

Poucet B, Benhamou S (1997) The neuropsychology of spatial cognition in the rat. Crit Rev Neurobiol 11:101–120

Poucet B, Herrmann T (2001) Exploratory patterns of rats on a complex maze provide evidence for topological coding. Behav Proc 53:155–162

Poucet B, Chapuis N, Durup M, Thinus-Blanc C (1986) A study of exploratory behaviour as an index of spatial knowledge in hamsters. Anim Learn Behav 14:93–100

Poucet B, Bolson B, Herrmann T (1990) Spatial behavior of septal and normal rats on alternate route maze problems. Q J Exp Psychol 42B:369–384

Save E, Poucet B, Foreman N, Buhot MC (1992) Object exploration and reactions to spatial and non spatial changes in hooded rats following damage to parietal cortex or dorsal hippocampus. Behav Neurosci 106:447–456

Schmajuk NA, Thieme AD (1992) Purposive behavior and cognitive mapping: a neural network model. Biol Cybern 67:165–174

Schmajuk NA, Thieme AD, Blair HT (1993) Maps, routes, and the hippocampus: a neural network approach. Hippocampus 3:387–400

Thinus-Blanc C, Bouzouba L, Chaix C, Chapuis N, Durup M, Poucet B (1987) A study of spatial parameters encoded during exploration in hamsters. J Exp Psychol Anim Behav Proc 13:418–427

Trullier O, Meyer JA (2000) Animat navigation using a cognitive graph. Biol Cybern 83:271–285

Vauclair J (1980) Etude ontogénétique de l'exploration chez le Hamster doré. Behaviour 73:205–218

Yeap WK, Jefferies ME (1999) Computing a representation of the local environment. Artif Intell 107:265–301