HIPPOCAMPUS 17:595–599 (2007)

RAPID COMMUNICATION

Spontaneous Navigational Strategies and Performance in the Virtual Town

Nicole Etchamendy* and Veronique D. Bohbot

ABSTRACT: The 4-on-8 virtual maze provides evidence for variability in spontaneous strategy use during navigation. Functional magnetic resonance imaging (MRI) confirmed that these spatial and response strategies rely on the hippocampus and caudate nucleus memory systems, respectively. We asked whether the spontaneous use of a particular navigational strategy was associated with a particular ability to navigate in one's environment. We tested 30 young participants on the 4-on-8 virtual maze and we assessed their way finding ability in a virtual town. As expected, spatial learners performed well in the virtual town and the response learners, who never used external landmarks and relied purely on an egocentric strategy, performed poorly. Interestingly, a group who used the most efficient response strategy based on external landmarks in the 4-on-8 virtual maze, switched to the most efficient spatial strategy in the virtual town. Our data suggest that the best navigators are those who appropriately use spatial or response strategies depending on the demands of the task. © **2007 Wiley-Liss, Inc.**

KEY WORDS: spatial memory; hippocampus; virtual environment; learning; basal ganglia

INTRODUCTION

Successful navigation can be achieved with two known strategies, each dependent on separable brain areas. One strategy involves using knowledge of the relationships between environmental landmarks represented in the form of a cognitive map of the environment; the other strategy, termed stimulus-response learning, leads to automatic behavioral response, independent of the spatial relationships between external landmarks (Tolman, 1948; O'Keefe and Nadel, 1978). This study investigates the natural variability in the flexible use of spatial and response strategies according to the task requirements.

We previously developed the 4-on-8 virtual maze (Iaria et al., 2003), a task used to identify spontaneous navigational strategies. Participants were asked to retrieve objects from fixed locations in a virtual 8-arm radial maze located in an environment containing landmarks. The task could be performed using a spatial memory strategy or a nonspatial strategy thought to lead to automatic responses with practice (termed response strategy in the current paper). After three trials, a probe trial was presented where the landmarks were no longer visible in the environment; resulting in altered performance of spatial learners. We found that, in a cohort of 50 participants, 50% spontaneously used a spatial strategy (using landmarks) as found in rodents (McDonald and White, 1994) and, as expected, spatial learners performed poorly in the probe trial. Half of them shifted to a response strategy with repetitive training as previously reported in rats (Packard and McGaugh, 1996), whereas the other half persevered with a spatial strategy despite their poor performance at the time of the probe. The 50% remaining participants performed well in the probe trial as they used a response strategy. This latter group includes the participants using a pure egocentric strategy (i.e., ignoring all external landmarks and using a series of left and right turns from their own starting position as a reference) and those using a series of turns from an external landmark. Associated fMRI data showed that the hippocampus (HPC) was active only in spatial learners, whereas the caudate nucleus (CN) of the striatum was active in response learners (Iaria et al., 2003) as we had hypothesized based on research with rats. This was further supported by additional data showing that patients with damage to the medial temporal lobes who used a spatial strategy in the 4-on-8 virtual maze were significantly impaired on the training trials relative to patients who used a response strategy (Bohbot et al., 2004a). This was the first report extending conclusions originating from animal studies dissociating the role of the HPC and CN in spatial and response learning respectively.

Beyond these conclusions, a point of particular interest in this study was that spatial learners were slower and made significantly more errors at performing the task than response learners (basing their strategies on an external landmark or their own starting position), suggesting that the most efficient strategy on the 4-on-8 virtual maze was the response strategy. Whether or not they used external landmarks, response learners displayed a behavior that was adapted to the task demands whereas the spatial learners did not.

Department of Psychiatry, Memory and Motion Laboratory, Douglas Hospital Research Centre, McGill University, Verdun, Quebec, Canada
Grant sponsor: Canadian Institutes for Health Research; Grant number: 64381; Grant sponsor: Fonds de la Recherche en Santé du Québec; Grant numbers: 3234, 2828. Nicole Etchamendy has received a postdoctoral fellowship from the FRM (France).
*Correspondence to: Nicole Etchamendy, Centre de Neurosciences Intégratives et Cognitives Université Bordeaux 1-C.N.R.S. UMR-5228, Avenue des Facultés, 33405 Talence Cedex, France.
E-mail: etxamendi@hotmail.fr
Accepted for publication 28 March 2007
DOI 10.1002/hipo.20303
Published online 1 June 2007 in Wiley InterScience (www.interscience.wiley.com).

FIGURE 1. Two views of the virtual town showing a shop (top) and buildings (bottom). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

In line with these findings, Hartley et al. (2003) differentiated between tasks that could be solved using a response strategy (route following) and those that require the use of a cognitive map (i.e., way-finding). They showed that the HPC was significantly correlated to performance in way-finding requiring the use of a cognitive map in order to create shortcuts to a target location. In contrast, activation of the CN was significantly correlated to response learning in the route following task. Of particular interest, they showed that the best navigators showed optimal activation of the HPC in the way-finding task and an optimal activation of the CN in the route following task. Consistent with our results, this suggests that some participants were particularly more flexible, shifting efficiently from one system to another (HPC vs. CN) and used the adapted strategy according to the task demands (spatial vs. response strategy). Altogether, these studies suggest a natural interindividual variability in the use of the most efficient strategy (response vs. spatial) according to the cognitive requirement of a task. We further assessed the ability to flexibly use spatial and response learning by examining the performance of a cohort of 30 healthy participants in the 4-on-8 virtual maze, involving the use of a response strategy for optimal performance, and in the wayfinding version of the virtual town, requiring a cognitive mapping strategy for optimal performance (Fig. 1) (Hartley et al., 2003).

The debriefing reports (Table 1, translated from French) indicated that 20 of the 30 participants initially solved the 4-on-8 virtual maze using a spatial strategy. However, by the end of the test, 11 of these 20 participants shifted to a response strategy (shift group). The remaining 10 participants used a response strategy throughout the entire task. Among these 10 response learners, we identified half using their own starting position as a reference (the response-SP group), the other half used an external landmark as a reference point (the response-

TABLE 1.

Example of the debriefing reports collected at the end of the 4-on-8 task allowing a categorization of the participants according to the strategy they used to solve the task

Classification	Debriefing reports
Spatial	"I used the mountain and the small tree. In front of me, the path was closed, as well as the path to the right of the pine tree and the one in front of the sunset. When the landscape disappeared, I tried to reconstitute the scene in my head. After that, I continued using the same elements of the scenery to find my bearings."
Shift	"I used the pine tree, the other tree and the yellow sky. It was closed at the right of the pine tree, on both sides of the tree and in front of the yellow sky. After the landscape was gone, I learned the sequence of closed–opened."
Response-SP	"The starting position was always the same, the two paths in front of me were closed, at the left it was opened, then two paths were open, and the other again at the left was closed, finally I counted."
Response-EL	"I learned the sequence starting from the pine tree: closed, closed, open, and so on. I did not retain the [path] number."

EL group). During the probe trial, most of the participants had the impulse to look around before making their selection and lost their initial heading. Consequently, the pattern of visited arms was used to score errors on the probe trial instead of using the actual arms in absolute space. This was assessed by rotating the pattern of visited arms until we obtained the best match. This method allowed us to differentiate the individuals who had learned the pattern of arms, the response learners, from those who had used the spatial strategy. The analysis performed on these probe errors revealed significant main effect of group [analysis of variance (ANOVA), $F(3,26) = 3.38$; $P < 0.05$]. As expected, the spatial group made more errors than both the response-SP (post hoc comparison: $P < 0.05$) and the response-EL (post hoc comparison: $P < 0.05$) groups (Fig. 2a). On the other hand, the shift group was not different from the spatial group or from the two response groups. As we can see in Figure 2a, this group was composed of participants who changed their strategy before the probe and behaved as response learners during the probe (i.e., making fewer errors) and participants who modified their strategy after the probe and behaved as spatial individuals during the probe, (i.e., making more errors).

We then analyzed performance on the virtual town according to the strategy that was identified in the 4-on-8 virtual maze. The ANOVA revealed a significant main effect of group [$F(3,26) = 5.59$; $P < 0.01$]. Detailed post hoc comparisons indicated that those who spontaneously used a spatial strategy throughout the 4-on-8 virtual maze made significantly fewer errors when navigating in the virtual town (Fig. 2b) than the participants qualified as response-SP in the 4-on-8 virtual maze ($P < 0.05$). Interestingly, the participants using the response-EL strategy performed as well as the spatial participants in the virtual town and significantly better than the response-SP strategy group ($P < 0.05$).

Our study examined the participants' flexibility in their ability to use spatial memory in the virtual town, which is the best strategy to reach a target in the shortest path, and their ability to use response learning in the 4-on-8 virtual maze, which is the most efficient strategy in terms of latencies and errors. Response learners were further dissociated into those who used landmarks and those who used the starting position, the only egocentric group (response-EL vs. response-SP).

We found that the best navigators in the virtual town were the spatial learners and the response-EL learners. In contrast, the response-SP learners were significantly worse relative to the response-EL learners and to the spatial learners. The participants who shifted from a spatial strategy to a response strategy on the 4-on-8 task did not perform statistically differently from the best navigators in the virtual town (i.e., the response-EL participants); however, the mean number of errors made was larger in absolute value and is associated with a higher inter-individual variability suggesting that this group is composed of participants who did not use the most efficient strategy in the way-finding task.

In sum, the spatial learners showed less flexibility because they used the spatial strategy in both tasks, although the response strategy was more efficient in the 4-on-8 virtual maze. The response-SP learners were also less flexible because they used the response strategy in both tasks, although it was not efficient in the virtual town as indicated by poor performance. In contrast to spatial learners and response-SP learners, the individuals in the shift group were able to use either a response or a spatial strategy but not always with an appropriate manner according to the task requirements. Finally, the individuals belonging to the response-EL group were the only participants to flexibly use the most adaptive strategy in either task: They used a response strategy, efficient in the 4-on-8 virtual maze and they performed accurately in the "way-finding task" using an efficient spatial strategy. In both tasks, the response-EL group used external landmarks but in different ways. Specifically, they used directional from a landmark in order to develop a response strategy adapted to the 4-on-8 task or they established relationships between several landmarks to build a cognitive map and navigate in the town. The use of external landmarks played a major role in distinguishing the response-EL group from the response-SP group who did not use external landmarks and used a purely egocentric strategy. The response-EL group also dissociated themselves from individuals that

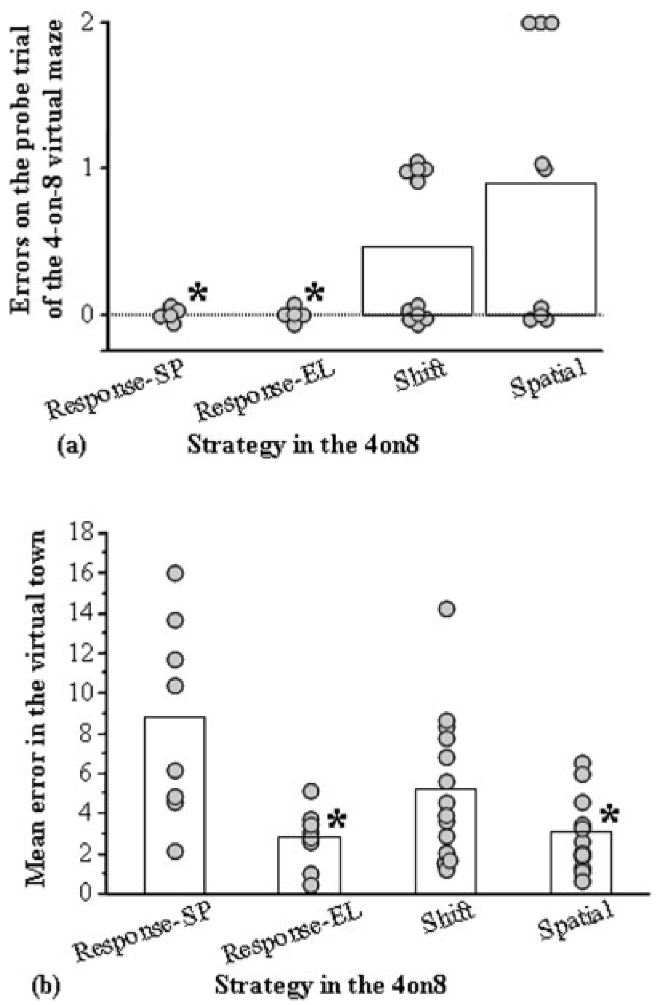

FIGURE 2. (a) Behavioral results of the 4-on-8 virtual maze: The number of errors made while performing the probe trial averaged across participants in the spatial, shift, response-start position (SP) and response-external landmark (EL) groups. *: *P* < 0.05 vs. spatial group. Note that the probe errors were scored by rotating the pattern of visited arms until we obtained the best fit, reducing the maximum number of errors to 2. Probe errors of the shift group show two distinct clusters: those who shifted from the spatial to the response strategy before the probe making fewer errors than those who shifted after the probe. (b) Performance on the virtual town as a function of the strategy used in the 4-on-8 virtual maze. Error was calculated as distance traveled beyond the shortest route. This figure shows that the response-EL group (i.e., the group that counted open and closed paths from an external landmark) and the spatial group performed well dissociating themselves from the response-SP group (i.e., the group that counted from their own starting position). *: *P* < 0.05 vs. response-SP group. The bars show the standard error of the mean.

shifted strategies they used the most adaptive strategies in either task, whereas the shift group did not.

These data corroborate the observations made by Hartley et al. (2003) suggesting that the best navigators were those using one memory system or another (spatial/HPC vs. response/CN) according to the task requirements. The next question consists in exploring the factors contributing to the variability in the flexible use of a given strategy. Maguire et al. (2000) found that experienced taxi drivers in London had greater gray matter density in the posterior HPC relative to non taxi drivers. On the other hand, the best navigators in the virtual town did not show greater gray matter density in the HPC (Maguire et al., 2003). In a preliminary report, we showed that the inflexible groups, the spatial and the responses-SP group, were biased towards a given strategy due to higher gray matter in the HPC and CN, respectively (Bohbot et al., 2004b). Altogether, these studies suggest that the best navigators in our study, the response-EL group, may show greater flexibility due to average levels of gray matter in the HPC and CN.

DETAILED METHODS

A commercially available computer game (UT2003, Epic Games) was used to create a new version of the virtual tasks, which were administered on a 19-in. computer screen. Participants used a keypad with forward, backward, left, and right turn buttons to navigate.

4-ON-8 Virtual MAZE

For the most part, the administration of the task remained the same as the original study (Iaria et al., 2003). During training trials, participants were told to retrieve objects from four of eight arms and were told to remember which arms they visited in order to avoid them in the next trial. After three training trials, a probe trial was administered. The objective remained the same (retrieve the four objects); however the landscape was concealed to hide the landmarks. If participants were using a spatial strategy (requiring landmarks) this change in the environment should impair performance. In contrast, this change should not affect the performance of nonspatial learners. A fifth training trial was administered after the probe to identify those who would shift strategies.

At the end of the experiment, participants were debriefed and were asked how they solved the task. They were then categorized as using a response strategy if they associated the arms with numbers or letters, or counted the arms from a single starting point. If they used at least two landmarks and did not mention a response strategy, they were categorized as using spatial memory. Participants who mentioned using several landmarks at the start and later shifted to counting were placed into the "shift group". We measured the errors made during the test and the time spent to perform the tasks in each section.

Way-finding in the Virtual Town

This protocol was modeled after the virtual town published by Hartley et al. (2003). The virtual town we built (see Fig. 1) was composed of different buildings, houses, and alleys, including eight distinct landmarks (e.g., shops, cinema). The landmarks were arranged in such a way that from each landmark, no other landmark was visible. This prevented the use of a strategy based on sequential stimulus-response associations. A two-dimensional map of the town was used to calculate "ideal paths" (i.e., most direct routes) between pairs of landmarks.

Acquisition

To learn the topography of the town, participant freely explored for at least 20 min. Occasional verbal direction from the experimenter was necessary to ensure that (1) participants attended each landmark (2) each location was visited more than once, and (3) all the roadways were fully explored.

Probes trials

To assess their spatial representation of the town, participants were placed in front of a particular landmark location and were instructed to navigate to another indicated landmark taking the shortest path. Different probe trials were made so that any two landmarks were paired only once during the experiment. In addition, each of the eight landmarks was used only once as a starting position and once as a destination. This prevented the development of familiar routes. Participants completed eight probe trials. Performance was measured by comparing the path taken in each probe with the ideal path.

Research Participants

Thirty normal participants (18 females and 12 males matched in age; mean age: 26.8 $\pm$ 3.94 yr) were tested. None of the participants had a history of neurological disorders. The participants were graduate students, postdoctoral fellows, and medical doctors recruited at the Douglas. Informed consent was obtained in a manner approved by the local ethics committee. Participants were all given the two tasks and the order of task administration was counterbalanced across participants.

REFERENCES

Bohbot VD, Iaria G, Petrides M. 2004a. Hippocampal function and spatial memory: Evidence from functional neuroimaging in healthy participants and performance of patients with medial temporal lobe resections. Neuropsychology 18:418–425.

Bohbot VD, Thorndycraft B, Lerch J, Iaria G, Zijdenbos A. 2004b. Morphological differences in the hippocampus and caudate nucleus as a function of navigational strategies in normal healthy young volunteers. Soc. Neurosci Abstract Viewer/Itinerary Planner Program No 596.7.

Hartley T, Maguire EA, Spiers HJ, Burgess N. 2003. The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. Neuron 37:877–888.

Iaria G, Petrides M, Dagher A, Pike B, Bohbot VD. 2003. Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. J Neurosci 23:5945–5952.

Maguire EA, Gadian DG, Johnsrude IS, Good CD, Ashburner J, Frackowiak RS, Frith CD. 2000. Navigation-related structural change in the hippocampi of taxi drivers. Proc Natl Acad Sci USA 97:4398–4403.

Maguire EA, Spiers HJ, Good CD, Hartley T, Frackowiak RS, Burgess N. 2003. Navigation expertise and the human hippocampus: A structural brain imaging analysis. Hippocampus 13:250–259.

McDonald RJ, White NM. 1994. Parallel information processing in the water maze: Evidence for independent memory systems involving dorsal striatum and hippocampus. Behav Neural Biol 61:260–270.

O'Keefe J, Nadel L. 1978. The Hippocampus as a Cognitive Map. Oxford, Clarendon.

Packard MG, McGaugh JL. 1996. Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. Neurobiol Learn Mem 65:65–72.

Tolman EC. 1948. Cognitive maps in rats and men. Psychol Rev 55:189–208.