NeuroImage 53 (2010) 725–735

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Neural correlates of real-world route learning

Victor R. Schinazi *, Russell A. Epstein

Department of Psychology, Center for Cognitive Neuroscience, University of Pennsylvania, Philadelphia, PA 19104, USA

ARTICLE INFO

Article history:
Received 21 June 2010
Accepted 25 June 2010
Available online 11 July 2010

Keywords:
Route learning
Landmark
Navigation
Retrosplenial cortex
Parahippocampal cortex

ABSTRACT

Classical theories of spatial microgenesis (Siegel and White, 1975) posit that information about landmarks and the paths between them is acquired prior to the establishment of more holistic survey-level representations. To test this idea, we examined the neural and behavioral correlates of landmark and path encoding during a real-world route learning episode. Subjects were taught a novel 3 km route around the University of Pennsylvania campus and then brought to the laboratory where they performed a recognition task that required them to discriminate between on-route and off-route buildings. Each building was preceded by a masked prime, which could either be the building that immediately preceded the target building along the route or immediately succeeded it. Consistent with previous reports using a similar paradigm in a virtual environment (Janzen and Weststeijn, 2007), buildings at navigational decision points (DPs) were more easily recognized than non-DP buildings and recognition was facilitated by in-route vs. against-route primes. Functional magnetic resonance imaging (fMRI) data collected during the recognition task revealed two effects of interest: first, greater response to DP vs. non-DP buildings in a wide network of brain regions previously implicated in spatial processing; second, a significant interaction between building location (DP vs. non-DP) and route direction (in-route vs. against-route) in a retrosplenial/parietal-occipital sulcus region previously labeled the retrosplenial complex (RSC). These results indicate that newly learned real-world routes are coded in terms of paths between decision points and suggest that the RSC may be a critical locus for integrating landmark and path information.

Introduction

A strategy for successful navigation in large-scale environments is to follow routes defined by landmarks and the spatial relationships between them. Such a strategy is likely to be especially useful for urban navigation where landmarks are plentiful and the space is generally too large to be perceived in its entirety from any one vantage point. Siegel and White (1975) proposed that spatial knowledge develops in a series of stages where landmark and route knowledge are the precursors of survey knowledge; a scheme that has been labeled the dominant framework (Montello, 1998). Neuroscientific work on spatial navigation, on the other hand, has often focused on the systems that support flexible route generation using cognitive maps, or the following of "well-worn" routes that are coded in terms of stimulus-response contingencies, leaving the neural systems that encode newly learned routes, which are not yet well-worn or incorporated into a cognitive map, relatively unexplored. Here we address this lacuna by examining fMRI activity related to the coding of landmarks and spatial relationships between landmarks along a newly learned route.

Subjects were trained on a 3.8 km route through the University of Pennsylvania campus and the surrounding territory and later scanned while viewing photographs of buildings from the route. Our design is a real-world adaptation of a paradigm previously employed by Janzen and Weststeijn (2007) to study route learning in a virtual (i.e. videogame) environment. Using a masked prime recognition task, these authors found behavioral and neural evidence that individuals distinguish between objects at navigational decision points (i.e. locations such as intersections where there is possibility for a change in direction) and other objects; furthermore, the direction of travel is specifically encoded at decision points. fMRI results revealed that the posterior parahippocampal gyrus responded preferentially to objects at decision points and that the superior parietal lobe, anterior cingulate and right caudate nucleus were sensitive to the direction of travel at these locations (Janzen and van Turennout, 2004; Janzen and Weststeijn, 2007). Although we expected to replicate the behavioral results from this earlier study, we anticipated the possibility that different neural systems would be involved in route learning under natural learning conditions, where real-world routes are populated with ecologically valid landmarks (i.e. buildings rather than small objects on tabletops) and are too complex to be learned through stimulus-response contingencies.

We were especially interested in determining the involvement of the parahippocampal place area (PPA) (Epstein and Kanwisher, 1998) and retrosplenial complex (RSC) in landmark and route learning. The

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* Corresponding author. Department of Psychology, University of Pennsylvania, 3720 Walnut Street, Philadelphia, PA 19104, USA. Fax: +1 215 898 1892.
E-mail address: schinazi@sas.upenn.edu (V.R. Schinazi).

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doi:10.1016/j.neuroimage.2010.06.065

PPA and RSC respond preferentially to stimuli of potential navigational relevance, such landscapes, cityscapes and rooms, and are critical nodes of the larger network of regions that are typically activated during navigation tasks (Aguirre et al., 1996; Ghaem et al., 1997; Maguire et al., 1998; Hartley et al., 2003; Rosenbaum et al., 2004; Spiers and Maguire, 2007). Previous work suggests that the PPA plays a particularly important role in the coding of scenes and buildings (Epstein et al., 1999); furthermore, insofar as the PPA is coterminous with the posterior parahippocampal gyrus, the previous work on decision points suggests that its response to even nonscene/non-building objects can be modulated by the navigational relevance of these objects (Janzen and van Turennout, 2004; Janzen and Wegsteijn, 2007). The RSC, on the other hand, may play a key role in the coding of directional information that allows us to understand the spatial relationship between different locations (Sato et al., 2006; Byrne et al., 2007; Epstein, 2008). Thus, we predicted that PPA should respond strongly to buildings from the path, and we set out to determine if this response would be modulated by the position of buildings at decision points. We also set out to substantiate a possible role for RSC in the coding of path direction. To anticipate, both these predicted functions were supported and elaborated by the data.

Materials and methods

Subjects

Two experiments were performed. Sixteen subjects (4 right-handed males, 1 left-handed male, 11 RH females, median age 23 years, range 19–28) with normal or corrected-to-normal vision participated in Experiment 1 and 16 subjects meeting the same criteria (7 RH males, 1 LH male, 7 RH females, 1 LH female, median age 21 years, range 19–31) participated in Experiment 2. All subjects were recruited from the University of Pennsylvania community and had lived on campus for at least 1 year. Written informed consent was obtained according to the provisions set by the local institutional review board.

Materials

The study area consisted of a 3.8 km circuitous route around the University of Pennsylvania campus and surrounding area. A total of 180 buildings were located directly on the route (Fig. 1a). Of these, 85 were located at decision points (DPs) which were intersections where there was a possibility for a change in direction, while 95 were located at non-decision points (NDPs). Ninety additional buildings not directly on the route but located within the general vicinity were selected as foils. A digital camera was used to obtain color photographs (768 × 768 pixels) of all 270 buildings for use as stimuli. Visual masks (90 total) were constructed by scrambling route and foil images in a 30 × 30 grid and then randomly combining fragments across scrambled images.

Design and procedure

Both experiments began with a study phase during which subjects were guided along a preset route and asked to remember both the route and all the buildings located directly along it. They were told that they were being trained to become future tour guides for the University and that this was the route they would show visitors and prospective students. They were also told that there would be many buildings along the route and that they should pay close attention and do their best to remember as many of them as possible. Upon completing a circuit, subjects were asked to reproduce the route by guiding the experimenter. If subjects wandered off course, they were stopped by the experimenter who explained the error and put them back on track. Subjects were very accurate in reproducing the route with only 1 subject committing a small deviation in the West portion of the route. The learning phase lasted for 90 min (45 min for each circuit).

The testing phase began immediately after subjects completed the second pass through the circuit. In Experiment 1, subjects were brought to the laboratory where behavioral data was obtained. In Experiment 2, subjects were brought directly to the MRI scanner located at the University of Pennsylvania Hospital where both behavioral and fMRI data were obtained. Subjects were not informed of the major hypotheses at any point during the experiment.

Experiment 1 (behavioral)

Subjects were tested using a masked prime recognition task similar to the one implemented by Janzen and colleagues (Janzen, 2006; Janzen and Wegsteijn, 2007). On each trial subjects viewed a photograph of a building and used the keyboard to indicate whether it was directly on the route or not. Each target building was preceded by a masked prime, which could either be a building that immediately preceded or followed the target along the route (Fig. 2). More specifically, each trial began with a fixation cross centered on the screen (100 ms); followed by a mask (150 ms), the prime building (40 ms), and then a second mask (60 ms). After a brief interval (100 ms), the target building appeared on the screen and remained visible for 5000 ms or until the subject responded. The next trial began immediately afterwards. Subjects were instructed to respond as quickly as possible while maintaining accuracy. Post-hoc questioning revealed that subjects were not consciously aware of the masked primes.

The 180 on-route buildings allowed for a total of 90 prime-target pairs. These were assigned to four conditions taking into account the order in which buildings appeared along the route (in-route vs. against-route) and whether the target building was located at a decision point or not (Fig. 1b). In the *in-route decision point* and the *in-route non-decision point* conditions (45 pairs in all) the prime building was the building immediately preceding the target building on the same side of the street. In the *against-route decision point* and *against-route non-decision point* conditions (45 pairs in all) the prime building was the building immediately following the target building on the same side of the street. These conditions were counterbalanced across subjects so that each building appeared equally often as an in-route prime, in-route target, against-route prime and against-route target. Decision points could either involve turns or straight continuation; turns vs. non-turns. These were closely balanced in number (DP turn = 42; DP straight = 43). In addition to these 90 prime-target trials, 45 foil trials were created by randomly pairing images of the 90 buildings that were not directly on the route. Event order was randomized for each subject.

After the main experiment, subjects were asked to rate their familiarity with each individual building along the route. Subjects viewed photographs of the 180 buildings presented on a desktop computer and rated their pre-experimental familiarity with each building on a scale from 1 to 5, with 1 being "not familiar" to 5 being "very familiar."

Experiment 2 (fMRI)

The experiment was essentially the same as Experiment 1 but performed in the fMRI scanner. In particular, the task, stimuli, and presentation parameters were identical, except for the fact that target buildings in Experiment 2 remained on the screen for a fixed interval of 2000 ms rather than disappearing after the subject made a response. This ensured that fMRI response differences between conditions could not be attributed to differences in the length of the physical stimulation. The next trial then began after a 3550 ms fixation interval, making each trial 6 s long.

The experiment consisted of three experimental scans followed by two functional localizer scans. Experimental scans ranged from 6 min