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Cognition 94 (2004) 39–75
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Geometric determinants of human spatial memory

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Received 14 February 2003; revised 23 October 2003; accepted 12 December 2003

Abstract

Geometric alterations to the boundaries of a virtual environment were used to investigate the representations underlying human spatial memory. Subjects encountered a cue object in a simple rectangular enclosure, with distant landmarks for orientation. After a brief delay, during which they were removed from the arena, subjects were returned to it at a new location and orientation and asked to mark the place where the cue had been. On some trials the geometry (size, aspect ratio) of the arena was varied between presentation and testing. Responses tended to lie somewhere between a location that maintained *fixed distances* from nearby walls and a location that maintained *fixed ratios* of the distances between opposing walls. The former were more common after expansions and for cued locations nearer to the edge while the latter were more common after contractions and for locations nearer to the center. The spatial distributions of responses predicted by various simple geometric models were compared to the data. The best fitting model was one derived from the response properties of 'place cells' in the rat hippocampus, which matches the 'proximities' $1/(d + c)$ of the cue to the four walls of the arena, where d is the distance to a wall and c is a global constant. Subjects also tended to adopt the same orientation at presentation and testing, although this was not due to using a view matching strategy, which could be ruled out in 50% of responses. Disoriented responses were most often seen where the cued location was near the center of the arena or where the long axis of a rectangular arena was changed between presentation and testing, suggesting that the geometry of the arena acts as a weak cue to orientation. Overall, the results suggest a process of visual landmark matching to determine orientation, combined with an abstract representation of the proximity of the cued location to the walls of the arena consistent with the neural representation of location in the hippocampus.
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Keywords: Hippocampus; Path integration; Cognitive map; Computational model

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doi:10.1016/j.cognition.2003.12.001

1. Introduction

The ability to return to a previously visited location is an important part of everyday behavior. Where the location is either unmarked or out of sight, this ability clearly depends on memory. However, several different forms of representation have been postulated for spatial memory, which we outline below. We then discuss evidence from cognitive neuroscience, which suggests that, far from being mutually exclusive, all of these postulated forms of representation might be available in the brain. In the final two sections of the introduction we review previous behavioral investigations of the nature of the representations in spatial memory and then outline the rationale for the experiment presented here.

One of our aims is to build a bridge between the behavioral and neurophysiological data regarding spatial representations. By manipulating the aspect ratio of a rectangular arena, O'Keefe and Burgess (1996) showed how the neural representation of location in the rat hippocampus was determined by geometric properties of the environment. Here we apply the same manipulations in a behavioral investigation of human spatial memory. The effects of these manipulations on the spatial distribution of subjects' responses are then compared with the effects predicted by alternative geometric models, including one derived from the neurophysiological experiment (Burgess & O'Keefe, 1996; Hartley, Burgess, Lever, Cacucci, & O'Keefe, 2000).

1.1. Representations in spatial memory

1.1.1. Perceptual representations

Perhaps the simplest type of model of spatial memory stresses the use of perceptual representations. For example, one's memory for a location and the relationship of objects near to it could be stored as a set of visual 'snapshots' (Roskos-Ewoldsen, McNamara, Shelton, & Carr, 1998). The potential uses of such perceptual memories are not limited to the recognition of previously experienced scenes. For instance, they could support object recognition from novel viewpoints (see Ullman, 1998). When combined with an ability to assess how well stored snapshots match the current sensory scene, they could also support navigation, providing some aspect of the target is visible from the starting location (Cartwright & Collett, 1982).

1.1.2. Path integration

'Path integration' models (Mittelstaedt & Mittelstaedt, 1980) use a cumulative record of the movements made by the subject since visiting a given location to maintain and update the vector back to the location during movement of the subject. Since this vector is relative to the subject's body, path integration can be thought of as a type of 'egocentric' representation of the location from which the movement started. These models often stress the role of idiothetic information (e.g. vestibular and proprioceptive information) in tracking movement, though external feedback from self-motion (e.g. optic flow) could also play a role. However self-motion is computed, it is clear that any errors in the process will be cumulative, making path integration inaccurate for all but the shortest, simplest paths. For path integration to be of use over more elaborate paths or longer durations, these

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