

Spatial imagery of novel places based on visual scene transformation

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Abstract

The hippocampus is known to maintain memories of object-place associations that can produce a scene expectation at a novel viewpoint. To implement such capabilities, the memorized distances and directions of an object from the viewer at a fixed location should be integrated with the imaginary displacement to the new viewpoint. However, neural dynamics of such scene expectation at the novel viewpoint have not been discussed. In this study, we propose a method of coding novel places based on visual scene transformation as a component of the object-place memory in the hippocampus. In this coding, a novel place is represented by a transformed version of a viewer's scene with imaginary displacement. When the places of individual objects are stored with the coding in the hippocampus, the object's displacement at the imaginary viewpoint can be evaluated through the comparison of a transformed viewer's scene with the stored scene. Results of computer experiments demonstrated that the coding successfully produced scene expectation of a three object arrangement at a novel viewpoint. Such the scene expectation was retained even without similarities between the imaginary scene and the real scene at the location, where the imaginary scenes only functioned as indices to denote the topographical relationship between object locations. The results suggest that the hippocampus uses the place coding based on scene transformation and implements the spatial imagery of object-place associations from the novel viewpoint.

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1. Introduction

The hippocampus has a beautiful cellular organization and a clear functional role in memory (Aggleton & Brown, 1999; O'Keefe & Nadel, 1978; Squire, 1992). In rodents, the memory in the hippocampus has been characterized as spatial in association with the findings of place cells (O'Keefe & Nadel, 1978), while the memory in the human hippocampus, on the other hand, has been characterized as episodic (Scoville & Milner, 1957) (i.e., the memory of personal

experiences in daily life). To have a common understanding of the hippocampus, the object-place memory paradigm has been used to investigate hippocampal memory in humans (Cave & Squire, 1991; King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002; Smith & Milner, 1981; Stepankova, Fenton, Pastalkova, Kalina, & Bohbot, 2004), monkeys (Gaffan, 1994; Rolls, 1999) and rodents (Eacott & Norman, 2004). The object-place memory is a simplified version of an episodic memory model consisting of "what", "where" and "when" (Tulving, 1983), and the afferent projections to the hippocampus is in good agreement with the functional requirements for the hippocampus to maintain the object-place memory, i.e., the hippocampus receives a convergent projection of the object information from the ventral visual pathway and spatial

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information from dorsal visual pathway (Suzuki & Amaral, 1994). The object-place memory paradigm is, therefore, available for investigating the neural basis of hippocampal memory (Eichenbaum, Yonelinas, & Ranganath, 2007; Mishkin, Suzuki, Gadian, & Vargha-Khadem, 1997).

In humans, a reconstruction task has been used to test neural mechanism of the object-place memory in the hippocampus (Cave & Squire, 1991; Smith & Milner, 1981). In this task, the subject is asked to remember a dozen objects and their locations on table in a short period of time. The objects are removed from the table and, after a delay period, the subject is asked to reconstruct the object arrangement according to their memory. When the hippocampus is damaged, the subject has great difficulty in performing this task. King et al. (2002) demonstrated that a subject with hippocampal damage is further characterized by problems in the recognition of object-place association from an unexperienced viewpoint based on memory. Such problem was only found in a short-term delayed-match-to sample task but was not found in a concurrent-match-to-sample task (Hartley et al., 2007). These evidences show that the hippocampus is necessary for reconstructing object-place associations at novel viewpoint (Fig. 1).

Cognitive map theory (O’Keefe & Nadel, 1978) has been a basis of the computational network models of the hippocampus (Burgess, Recce, & O’Keefe, 1994; Byrne, Becker, & Burgess, 2007; Hasselmo, Bodelón, & Wyble, 2002; Muller, Kubie, & Saypoff, 1991; Samsonovich & McNaughton, 1997; Wagatsuma & Yamaguchi, 2004) where the environmental memory is maintained by synaptic weights between place cells. Together with recent discovery of the grid cells (Hafting, Fyhn, Molden, Moser, & Moser, 2005), these models are developed in terms of neural coding (Burgess, 2008; Hasselmo, 2009; Molter & Yamaguchi, 2008). On the other hand, the models of the object-place memory (Byrne et al., 2007; Rolls, Stringer, & Trappenberg, 2002; Sato & Yamaguchi, 2005) include non-spatial in addition to place information to represent the complexity of the environment. The above network models represent places by using the synaptic weights of the place cells assumed to be learned during an encoding period and thus, these models

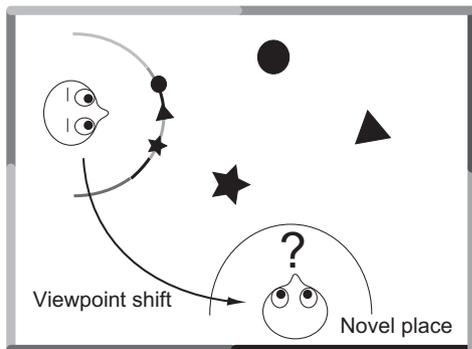


Fig. 1. Viewpoint shift to the object-place memory. The subject is asked to imagine the object arrangement at the novel place.

cannot code novel places before their learning has taken place.

In the rodent experiments, the place cell selectivity has been known to appear also in a novel environment (Hill, 1978). This indicates that the place cells are formed by some topographical information from the external environment. Hartley, Burgess, Lever, Cacucci, and O’Keefe (2000) proposed that place cell firings can be modeled using the sums of cortical inputs from the boundary vector cells (BVCs). It is hypothesized that BVCs respond whenever an environmental boundary is at a particular distance and allocentric direction from the animal. Recently BVCs are also found to exist in the subiculum (Lever, Burton, Jeewajee, O’Keefe, & Burgess, 2009). By using BVCs, Byrne et al. (2007) proposed a neural network model of mental navigation where the reactivation of the place cells in a cognitive map are updated by motor efferent signals. The model is unique in the computation of the spatial imagery of the environment, while the imagery is limited only in visited places. While the novel places cannot be represented by the reactivation of place cells. Some neural representation beyond BVCs should be considered to code novel places.

What are the necessary conditions for the coding of novel places that are available in spatial imagery? The successful coding is considered to satisfy the following three properties. (1) *Transformability*: The remembered place code should be able to be transformed to another place code by the imaginary displacement of a motor efferent signal. The transformation should be a one-to-one function mapping the place code to the displacement (Fig. 2a), otherwise different displacements can result in the same place code during imagery. (2) *Comparability*: An arbitrary

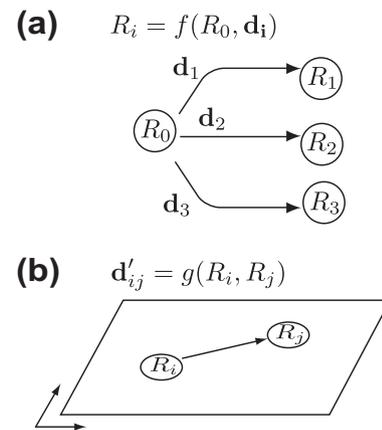


Fig. 2. Requirements of the putative place coding that is applicable to code the novel places. (a) A remembered place code, R_0 , can be transformed by a function, f , with an imaginary displacement, \mathbf{d}_1 to an unexperienced place representation, R_i . Different displacements, \mathbf{d}_1 , \mathbf{d}_2 and \mathbf{d}_3 should result in different place representations, R_1 , R_2 and R_3 . (b) Two place codings, R_i and R_j , can be compared to produce a displacement between them, $\mathbf{d}'_{ij} = g(R_i, R_j)$, where g is the displacement function. This function should be applicable to the comparison of two place codes transformed by different place codes, such as $R_i = f(R_0, \mathbf{d}_1)$ and $R_j = f(R_0, \mathbf{d}_2)$. Thus, the function need not to be the inverse function of the above transformation, $g(R_i, R_j) \neq f^{-1}(R_i, R_0)$.

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