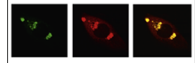


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Research Report

The entorhinal map of space [☆]

Kei M. Igarashi

Department of Anatomy and Neurobiology, University of California, Irvine, CA 92697, United States

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ABSTRACT

How do we know where we are, and how do we remember the places we visited? Since the discovery of place cells in 1971, our understanding of the brain's maps of external space has exploded. Yet the origin of the place-cell signal remained elusive. The discovery of grid cells in the medial entorhinal cortex (MEC) in 2005 put place cells in a context, since the existence of grid cells pointed to circuit mechanisms that might explain the formation of place cells. In this review, I shall review recent experimental and theoretical advances in the understanding of how space is mapped in the medial entorhinal cortex. I will also review recent studies of interactions between hippocampus and the lateral entorhinal cortex (LEC). Research on spatial mapping in the hippocampal-entorhinal system provides a fundament for future attempts to decipher some of the neural-circuit codes of the cortex.

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1. Introduction

The hippocampal region, a brain complex containing the hippocampus, subiculum, and entorhinal cortex (EC), is part of the medial temporal cortex in humans, and stretches through the posterior half of the cortex in the rodent brain (Fig. 1A). Because this region, especially the hippocampus, has a distinct cytoarchitecture, it has attracted anatomists since the first half of the twentieth century (Ramón y Cajal, 1911; Lorente de Nó, 1934). It was not until the second half of the century, however, that studies started to throw light on the function of this region. The first major breakthrough was a report by Scoville and Milner (Scoville and Milner, 1957) on memory loss in patient Henry Molaison (also widely known as H.M.), who had his hippocampal regions surgically removed for the treatment of severe epilepsy. The work indicated that the hippocampus and the entorhinal cortex (EC) play critical roles in the formation of declarative

memory, a type of memory that can be consciously recalled such as episodes and facts (Milner et al., 1968; Squire, 1992). Subsequent studies indicated that H.M. as well as other patients with temporal lobectomy also had impairments in spatial navigation and visual maze tasks (Milner et al., 1968; O'Keefe and Nadel, 1978).

Since the early studies of H.M., the hippocampus has had a magnetic impact on those interested in the cellular mechanisms of memory and spatial navigation. The studies of H.M. were followed almost two decades later by the discovery of place cells in the hippocampus (O'Keefe and Dostrovsky, 1971). O'Keefe and Dostrovsky thought it would be informative to study the neuronal correlates of memory by recording neuronal spike activity from the hippocampus during behavior. They implanted miniature electrodes in the hippocampus of rats and recorded activity from individual neurons while the rats moved around in the environment. Many of the cells they recorded fired specifically when the rat was at a

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E-mail address: igarashi.uci@gmail.com

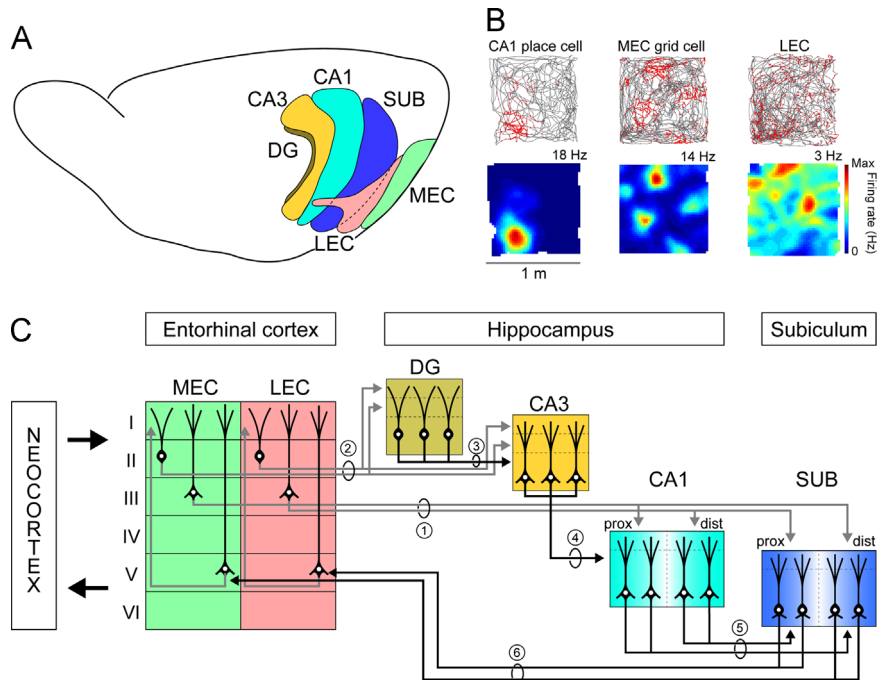


Fig. 1 – Architecture of the rat hippocampal regions. (A) Schematic showing lateral view of key hippocampal regions in the rat brain. The regions include hippocampal subfields CA1, CA3 and dentate gyrus (DG), as well as the subiculum, medial entorhinal cortex (MEC) and the lateral entorhinal cortex (LEC). Modified from (van Strien et al., 2009) with permission. **(B)** An example place cell in the CA1 (left), an example grid cell in the MEC (middle), and a representative cell with low spatial information in the LEC. Firing rate maps of spikes recorded in 1 m square box are shown. Top, trajectory of animal (gray) with spike positions superimposed (red). Bottom, color-coded rate maps. Color scale to the right. Peak firing rates (Hz) are indicated on top right and shown in red color. **(C)** Diagram of the major connections of the rat hippocampal formation. The hippocampus receives and sends information from the neocortex via entorhinal cortex. MEC and LEC project to CA1 through direct and indirect pathways. In the direct pathway (1), layer III cells in MEC largely project to proximal CA1 (prox), whereas layer III cells in LEC project to distal CA1 (dist). By contrast, in the indirect pathway, axons of layer II cells in MEC and LEC (2) converge on the same population of cells in the dentate gyrus (DG) and CA3. This mixed information in DG and CA3 is conveyed to CA1 via mossy fibers (3) and Schaffer collaterals (4). Output from CA1 is conveyed to entorhinal cortex mainly via the subiculum (SUB). In this output, information from proximal CA1 is conveyed to MEC via the distal part of subiculum, whereas distal CA1 projects to LEC via the proximal part of the subiculum ((5) and (6)). Modified from (Witter and Amaral, 2004) with permission.

certain location (O'Keefe and Dostrovsky, 1971) (Fig. 1A and B). O'Keefe and Dostrovsky called these cells place cells. Different place cells fired at different locations such that, as a population, place cells provided an accurate spatial map – a 'cognitive map' – of where the animal is at any given time. Following this finding, O'Keefe and Nadel (1978) investigated the rich literature on behavioral impairments following hippocampal lesions and concluded that most findings could be summarized as showing a role for the hippocampus in spatial functions (O'Keefe and Nadel, 1978). Their cognitive map theory was controversial for more than two decades, given the apparent non-spatial impairments of human patients with hippocampal lesions, but the diverging views have finally been reconciled by the recognition that space and declarative memory are tightly coupled. Suppose for example that you have lost your purse: you may recall back the moment last time you saw the purse, and you would try to remember one by one the places you visited and what you did there. Your memory typically involves spatial navigation, and this spatial component may serve as a framework of your memory. The hippocampus may use space as a scaffold for

most types of memories (O'Keefe and Nadel, 1978; Leutgeb et al., 2005; Buzsaki and Moser, 2013).

2. Grid cells in the medial entorhinal cortex

The discovery of place cells in 1971 raised a fundamental question: how is the activity of place cells generated? Is it generated intrinsically in the hippocampus, or does it reflect external inputs to the hippocampus? The hippocampus contains a strong excitatory feedforward circuit consisting of dentate gyrus, CA3 and CA1 (Fig. 1C) (Ramón y Cajal, 1911; Witter and Amaral, 2004). Most of its external cortical input to the hippocampus comes from the EC, and the hippocampus also sends much of its cortical output back to the EC. The EC interfaces the hippocampus with a number of cortical regions. In general, superficial layers of EC project to the hippocampus, whereas output from the hippocampus is sent back to the deep layers of the EC, which in turn project to the superficial layers of the EC, thus forming a loop circuit (Kloosterman et al., 2003; van Haefen et al., 2003). The

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