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Task Demands Predict a Dynamic Switch in the Content of Awake Hippocampal Replay

Highlights

- Place cell replay content varies between periods of task engagement and disengagement
- Upon arrival/before departure from reward sites, replay depicts task-relevant places
- No such bias was observed during periods of extended immobility
- Grid cells from deep MEC were coherent with place cells during extended stops

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In Brief

Ólafsdóttir et al. found that, upon arrival at and before departure from reward sites, but not during immobility, hippocampal replay depicts places related to current task demands. Occurrence of task-focused replay predicts decision accuracy. Grid cells were only coherent with replay during immobility.



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Task Demands Predict a Dynamic Switch in the Content of Awake Hippocampal Replay

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SUMMARY

Reactivation of hippocampal place cell sequences during behavioral immobility and rest has been linked with both memory consolidation and navigational planning. Yet it remains to be investigated whether these functions are temporally segregated, occurring during different behavioral states. During a self-paced spatial task, awake hippocampal replay occurring either immediately before movement toward a reward location or just after arrival at a reward location preferentially involved cells consistent with the current trajectory. In contrast, during periods of extended immobility, no such biases were evident. Notably, the occurrence of task-focused reactivations predicted the accuracy of subsequent spatial decisions. Additionally, during immobility, but not periods preceding or succeeding movement, grid cells in deep layers of the entorhinal cortex replayed coherently with the hippocampus. Thus, hippocampal reactivations dynamically and abruptly switch between operational modes in response to task demands, plausibly moving from a state favoring navigational planning to one geared toward memory consolidation.

INTRODUCTION

Prominent theories of hippocampal function place it at the center of networks supporting memory and navigation (O'Keefe and Nadel, 1978; Scoville and Milner, 1957). The principal cell of the hippocampus is the place cell, whose activity during locomotion encodes the animal's self-location via spatially localized firing fields (place fields) (O'Keefe and Dostrovsky, 1971). However, during non-rapid eye movement (non-REM) sleep and pauses in locomotion, when sharp-wave ripple complexes (SWRs) transiently dominate the hippocampal local field potential (LFP) (Buzsáki et al., 1992; O'Keefe and Nadel, 1978), place cell activity de-couples from the animal's current location, reactivating past or future spatial trajectories (replay) (Foster and Wilson, 2006; Lee and Wilson, 2002; Wilson and McNaughton, 1994).

At the time of discovery, replay was proposed as the mechanism supporting systems-level memory consolidation (Wilson and McNaughton, 1994), the process by which memories are transferred out of the hippocampus, becoming less susceptible to hippocampal damage (Marr, 1971; Scoville and Milner, 1957). Consistent with this hypothesis, replay typically reflects recent experiences, particularly novel ones (Cheng and Frank, 2008; Foster and Wilson, 2006; O'Neill et al., 2008; van de Ven et al., 2016), is dependent on the NMDA receptor (Dupret et al., 2010; Silva et al., 2015), and is associated with cortical reactivations (Ji and Wilson, 2007; Rothschild et al., 2017; Wierzynski et al., 2009). Indeed, cortical replay has been found to temporally lag the hippocampus (Ólafsdóttir et al., 2016; Rothschild et al., 2017), suggestive of information flow from the hippocampus to the cortex (Ólafsdóttir et al., 2016; Rothschild et al., 2017). Furthermore, numerous studies have shown that cortical LFP patterns associated with sleep, such as delta waves (Maingret et al., 2016; Mednick et al., 2013) and spindles (Johnson et al., 2010), are temporally coordinated with SWRs (Battaglia et al., 2004; Peyrache et al., 2011; Sirota et al., 2003), and they have indicated that cortico-hippocampal dialogue may be important for learning (Maingret et al., 2016). More generally, SWRs originate in the hippocampus (Buzsáki, 2015; Suzuki and Smith, 1985), propagate into the cortex (Chrobak and Buzsáki, 1994, 1996), and occur at a greater rate after learning (Eschenko et al., 2008). Elimination of SWRs during rest impairs spatial learning (Ego-Stengel and Wilson, 2010; Girardeau et al., 2009). Conversely, hippocampal reactivation during rest enhances learning (de Lavilléon et al., 2015; Rasch et al., 2007).

Nevertheless, it is now apparent that replay, and the roles attributed to it, are more diverse than first thought. While the role of replay during non-REM sleep (offline) in consolidation is well supported, the purpose of awake replay (online) is less clear. On one hand, online replay is modulated by environmental novelty (Cheng and Frank, 2008; Foster and Wilson, 2006) as well as changes in reward (Ambrose et al., 2016; Singer and Frank, 2009), and interference with online SWRs impairs the acquisition of spatial tasks (Jadhav et al., 2012), suggestive of a role in learning, if not also consolidation. However, online replay has also been linked with spatial planning and navigation (Foster and Knierim, 2012; Pfeiffer and Foster, 2013; Samsonovich and Ascoli, 2005), consistent with theoretical propositions suggesting replay as a mechanism for exploring potential routes or extracting goal-directed heading vectors (Bush et al., 2015; Erdem and Hasselmo, 2012, 2014; Gupta et al., 2010) and

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