

# Current Biology

## Overlap among Spatial Memories Triggers Repulsion of Hippocampal Representations

### Highlights

- Human hippocampal representations of overlapping spatial routes diverge with learning
- Representations of overlapping routes become less similar than non-overlapping routes
- Representational structure in the hippocampus sharply contrasts with other brain regions
- Hippocampal voxels exhibit divergence in relation to initial representational overlap

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### In Brief

Chanales et al. report that representations of overlapping spatial routes in the human hippocampus dramatically diverge with learning, ultimately becoming less similar than representations of non-overlapping routes. These findings suggest that event overlap triggers repulsion of hippocampal representations.

# Overlap among Spatial Memories Triggers Repulsion of Hippocampal Representations

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<http://dx.doi.org/10.1016/j.cub.2017.06.057>

## SUMMARY

Across the domains of spatial navigation and episodic memory, the hippocampus is thought to play a critical role in disambiguating (pattern separating) representations of overlapping events. However, it is not fully understood how and why hippocampal patterns become separated. Here, we test the idea that event overlap triggers a “repulsion” among hippocampal representations that develops over the course of learning. Using a naturalistic route-learning paradigm and spatiotemporal pattern analysis of human fMRI data, we found that hippocampal representations of overlapping routes gradually diverged with learning to the point that they became less similar than representations of non-overlapping events. In other words, the hippocampus not only disambiguated overlapping events but formed representations that “reversed” the objective similarity among routes. This finding, which was selective to the hippocampus, is not predicted by standard theoretical accounts of pattern separation. Critically, because the overlapping route stimuli that we used ultimately diverged (so that each route contained overlapping and non-overlapping segments), we were able to test whether the reversal effect was selective to the overlapping segments. Indeed, once overlapping routes diverged (eliminating spatial and visual similarity), hippocampal representations paradoxically became relatively *more similar*. Finally, using a novel analysis approach, we show that the degree to which individual hippocampal voxels were initially shared across route representations was predictive of the magnitude of learning-related separation. Collectively, these findings indicate that event overlap triggers a repulsion of hippocampal representations—a finding that provides critical mechanistic insight into how and why hippocampal representations become separated.

## INTRODUCTION

Distinct experiences often contain overlapping elements, creating the potential for memory interference. For example, a single loca-

tion (e.g., a living room) may be the site of many different experiences and corresponding memories. The hippocampus is widely thought to play a critical role in coding overlapping events such that interference is minimized. Compelling evidence for this function comes from intracranial recordings in rodents during spatial navigation. For example, when rodents alternate between left- and right-hand turns in a T maze, cells within the hippocampus differentially fire during the central stem (the overlapping path) according to whether the current route is a “right-turn” or “left-turn” route [1, 2]. Likewise, hippocampal place fields may completely remap with contextual changes in a rodent’s environment [3, 4]. In human studies of episodic memory, fMRI evidence indicates that visual stimuli that are shared across multiple event sequences are distinctly coded in the hippocampus according to the specific sequence to which they belong [5]. Although these studies and others have led to general agreement that the hippocampus forms distinct codes for overlapping experiences [6–16], the factors that trigger divergence of hippocampal representations are not fully understood.

The formation of distinct hippocampal representations is traditionally thought to be a result of sparse coding within the hippocampus [17–22]. Although there are not enough neurons in the hippocampus to entirely avoid representational overlap, sparse coding ensures that similar experiences are less likely to share neural units, thereby resulting in orthogonalized representations. Although this coding property of the hippocampus may play a critical role in reducing overlap during initial encoding, it is unlikely to provide a complete account of how hippocampal representations become distinct. In particular, overlap among hippocampal representations also changes with experience, suggesting learning-related factors that contribute to divergence. For example, hippocampal remapping in rodents may emerge over the course of learning [3, 23], and even the sensitivity of stable hippocampal place fields can be tuned by experience [24]. Similarly, experience-dependent divergence of hippocampal activity patterns has been observed in human fMRI data [6, 13, 25, 26]. Computational models suggest that one factor that drives learning-related divergence of hippocampal representations is competition [26–29]. When activity patterns overlap—which may reflect residual overlap following initial orthogonalization—this creates competition during learning that the hippocampus “solves” by reducing similarity among representations. This perspective makes a critical prediction: that overlapping representations should systematically move apart from one another over the course of learning. Indeed, the representational distance between overlapping events

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