

## Journal Club

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# Hippocampal Activity Patterns Reflect the Topology of Spaces: Evidence from Narrative Coding

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Review of Milivojevic et al.

Autobiographical memory has a hierarchical organization governed by personal narratives at multiple scales (Conway and Pleydell-Pearce, 2000), and analyses of large corpora of personal emails and visual images taken from people's daily lives have revealed such multiscale structures in real-world human contexts (Sreekumar et al., 2014, 2016). For example, a college student's life is governed by a long-timescale narrative of "getting a bachelor's degree." Within that narrative, at shorter timescales, students interact with various classmates in multiple locations on campus in both social and academic contexts. For example, a student might be in a chess club that meets in the library or might invite classmates to a party. Thus, the narratives that characterize our lives are often intertwined with shared features, such as people and locations. How are parallel and overlapping narrative contexts represented in the brain and how are they differentiated so we can switch between them in episodic memory? Further-

more, in the brain regions that distinguish between different narrative contexts, are components that are shared across contexts, such as characters and locations, also represented by distinct neuronal populations? How do the neural activity patterns corresponding to different narratives and their components evolve in time?

To answer these questions within the spatiotemporal confines of a laboratory, Milivojevic et al. (2016) recruited participants to watch the movie *Sliding Doors* while their brain activity was monitored using fMRI. Five minutes into the movie, the storyline diverges into two interwoven narratives with overlapping characters, locations, and objects. Helen, the main character, misses a train in narrative 1 but catches it in narrative 2. Most characters and locations are shared between the two narratives, and the narratives are interleaved in the movie, reducing confounds relating to temporal co-occurrence and visual similarity (both of which were further controlled for by statistical analyses). A whole-brain searchlight using representational similarity analysis (Kriegeskorte et al., 2008) revealed that hippocampal activity patterns differentiated between overall narrative contexts, as well as individual people and locations within those contexts. Furthermore, hippocampal activity corresponding to the two narratives gradually became more distinct over time. The authors discussed these results in the

light of known neural mechanisms of hippocampal pattern separation in spatial contexts.

Some studies have reported that the hippocampus is not involved in representing unitary items (e.g., Ross et al., 2017). Milivojevic et al. (2016) suggested that the character and location hippocampal representations in their study may be abstracted versions of those items across multiple experiences over the course of the movie and therefore may behave more like a gist or lower-level context for those items. Interestingly, the overall set of both cortical and subcortical regions that they report as being sensitive to locations and characters overlap with those that are engaged when people are probed about repeated personal events (for review on personal semantics, see Renoult et al., 2012, their Table 1). Although not a sufficient condition, the overlap lends some plausibility to the idea that the location and character representations reported by Milivojevic et al. (2016) are indeed abstractions over multiple presentations across the movie.

Milivojevic et al. (2016) report that narrative representations, but not location/character representations, diverged in the hippocampus over time. In contrast to hippocampal patterns, narrative representations in visual regions were more different in the beginning and converged across time. Milivojevic et al. (2016) speculated that the divergence of hippocampal

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narrative context representations may rely on similar mechanisms as those involved in the separation of representations of spatial environments with repeated experience. For example, Chanales et al. (2017) found that hippocampal representations for overlapping spatial routes diverged with learning, and diverged to a point where the activity patterns for overlapping routes were less similar than those for nonoverlapping routes, and this separation occurred preferentially in the hippocampal voxels that were initially shared across the overlapping routes.

As Eichenbaum and Cohen (2014) note, the hippocampus is unlikely to be dedicated to computations specific to spatial navigation. For instance, hippocampal place fields are sensitive to the context of abstract nonspatial task demands (Smith and Mizumori, 2006) and CA1 sequence coding extends beyond spatial sequences (Allen et al., 2016). What is more likely is that the hippocampus provides support for any computation that requires relational memory (Davachi, 2006). Dabaghian et al. (2014) demonstrated conclusively that hippocampal networks encode topological information (i.e., relationships between parts), such as contiguity in space, but not Cartesian information, such as locations and distances. Therefore, the hippocampus provides a general template for encoding relations between elements (i.e., the topology of a space); and as the results of Milivojevic et al. (2016) show, this seems to hold even for more abstract narrative spaces. Divergence of the overall narrative context representations across time may then arise due to remapping of hippocampal place cells as the authors suggest and what drives remapping may simply be the different topologies of the two narrative spaces because characters and locations, although shared, are encountered in different sequences and relations to one another in the two narratives.

Much is known about how the hippocampus represents information across spatiotemporal scales. There are neuroanatomical differences between the posterior and anterior parts of the hippocampus (pHPC and aHPC, respectively) in terms of both proportions of CA1–CA3 and DG subfields as well as their long-range connections to other parts of the brain that have led to hypotheses regarding functional specialization along the hippocampal long axis (for review, see Poppenk et al., 2013). The DG plays an important role in pattern separation and CA3 in pattern completion (for a recent review, see Knierim and Neunuebel,

2016); and given the higher ratio of DG/CA in the pHPC and lower ratio in the aHPC, Poppenk et al. (2013) proposed that the pHPC codes for events with sharper low-level detail via pattern separation whereas the aHPC codes at a broader scale for high-level gist by abstracting over multiple experiences via pattern completion. If this proposal is correct, one would expect higher-level narrative contexts as well as abstractions over multiple experiences of characters and locations to eventually be represented in the aHPC, whereas more specific location and characters to be represented in the pHPC. One possibility that Milivojevic et al. (2016) discuss is that pattern separation mechanisms may underlie the gradual separation of neural ensembles that represent the different narratives. Although on the surface, it seems difficult to reconcile this explanation with the prediction that aHPC mediated by pattern-completion codes for broader scale contexts (such as the narrative contexts experienced in the movie), pattern completion in the aHPC may play a role in associating an ongoing experience with a previously experienced context but remapping mediated by local topology (i.e., configurations of elements of ongoing experience in relation to each other) may lead to gradual separation of the neural ensembles that are activated by different contexts with accumulating experience.

The hippocampus is a remarkable piece of neural tissue, but any description of how it works is incomplete without specifying the role of the cortical regions that connect with it. The perirhinal cortex (PRC) exhibits preferential connectivity with the aHPC, whereas the parahippocampal cortex (PHC) shows preferential connectivity with the pHPC (Libby et al., 2012). Under conditions that remove the strong inhibition of inputs from these cortical regions to the hippocampal formation (de Curtis and Paré, 2004), this pattern of connectivity suggests that the aHPC receives fine-grained local configurational information (such as items and the associations between them) from the PRC, which gets bound to the relevant broad level context representation. Therefore, gradual changes in the broad level context representation may, at least in part, be driven by these cortical inputs. Fine-grained local representations in the pHPC, on the other hand, may be supported by precise local context/scene information it receives from the PHC (for review of the functional and neuroanatomical distinctions between PRC and

PHC-retrosplenial cortical systems, see Ranganath and Ritchey, 2012).

In conclusion, the results of Milivojevic et al. (2016) are consistent with the conceptualization of the hippocampus as providing a topological template for representations of spaces. The details of the interplay between pattern completion and separation, and how the different parts of the hippocampus and their subfields, along with their cortical counterparts act together to achieve separable representations of contexts that share component features are yet to be fully specified. However, the results of Milivojevic et al. (2016) constitute an important preliminary step toward understanding the mechanisms by which hierarchical context representations emerge in the brain over temporally extended naturalistic experience.

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