Trends in Cognitive Sciences

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Spotlight

Semantic Search as Pattern Completion across a Concept

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What role does the hippocampus play in semantic memory? In a recent paper, Cutler *et al.* use a vector space model of semantics to characterize semantic search deficits in hippocampal amnesia. We relate their findings to properties of the hippocampal neural code and to controversies regarding hippocampal contributions to cognition.

The hippocampus is known to play a crucial role in episodic memory, but its influence extends widely into other memory systems and cognitive domains [1,2]. This raises questions regarding the nature of hippocampal processing. Does the hippocampus contribute to online cognition only by retrieving stored hippocampal representations, or can it dynamically form new representations to support diverse cognitive functions? A version of this question is currently under debate in the episodic memory domain – is the hippocampus involved in remote episodic memory because it stores those memory traces, or because it helps to reconstruct cortically represented traces at the time of retrieval [3]?

In their recent paper, Cutler, Duff, and Polyn (hereafter, CDP) [4] ask a pertinent question in the semantic memory domain – how does the hippocampus contribute to the retrieval of remote semantic memories (i.e., our generalized knowledge of the world)? An earlier study by Klooster and Duff [5] reported that patients with hippocampal damage produce fewer responses than healthy controls on a semantic feature generation task in which a target concept is presented (e.g., ‘berry’) and one must generate as many features of the target as possible (e.g., ‘sweet’, ‘red’, ‘juicy’). To characterize these impairments in detail, CDP used a vector space model to reanalyze the data; this revealed differences in how amnesics and controls navigate semantic space. Vector space models of semantics leverage word co-occurrences in text to approximate the semantic similarity of the underlying concepts, thus allowing the authors to capture target-to-feature similarity (e.g., ‘berry’ and ‘sweet’) and feature-to-feature similarity (e.g., ‘sweet’ and ‘juicy’). Their analyses revealed that, relative to controls, the feature responses of amnesics tended to be closer in semantic space to the target concept. Although target-to-feature similarity decreased across successive responses for both groups, the controls exhibited a steeper decline in similarity such that later responses ranged farther from the target word in semantic space. In other words, the movement of amnesics through semantic space was more restricted.

CDP offer two interpretations of their results regarding the role of the hippocampus in semantic memory. In a memory curation hypothesis, the hippocampus contributes to the formation and updating of cortically stored semantic memory (consistent with systems consolidation theory), and damage to the hippocampus thus results in impoverished semantic representations over time. In this view, the semantic deficits of amnesics are due to degraded cortical semantic representations. A recent study [6] builds on Klooster and Duff [5] by adding a control group matched to the age of onset of hippocampal damage in the patient group. Age-of-onset controls and amnesics performed worse than current-age matched controls on semantic tasks, suggesting that the hippocampus does contribute to the continuous enrichment of semantic memory over long timescales. However, both control groups outperformed amnesics, implying an additional role for the hippocampus. The memory curation hypothesis may thus explain some of the observed deficits but not the full pattern of results.

CDP additionally propose the relational search hypothesis, in which deficits are caused by an impaired search process applied to intact semantic representations in neocortex. In episodic memory, the hippocampus is thought to rapidly bind representations of event elements together, and it could perform a similar role in semantic memory – quickly binding internal semantic elements for immediate use. We elaborate on this hypothesis by considering potential neural mechanisms and representations. What is the format of these hippocampal representations? How do they differ from semantic representations in neocortex? How do these interacting representations support semantic search?

We provide a framework for thinking about these questions in Figure 1. We represent a single concept as a network in which nodes represent features and edges represent their associations within that concept [7]. Concept representations (e.g., ‘berry’) in the cortex have rich structures in which some features (e.g., ‘sweet’, ‘red’) are more central whereas others are more peripheral (e.g., ‘seeds’, ‘sour’). This structure establishes feature–feature distances: ‘sweet’ and ‘red’ are closer in semantic space than ‘fuzzy’ and ‘seeds’ (Figure 1B). These cortically represented features are activated upon presentation of a concept label (e.g., ‘berry’), and then a binding of these features occurs in the hippocampus via the creation of a conjunctive code in dentate gyrus and CA3 subfields (Figure 1A). This binding operation would render the elements of the representation more fully connected than those in cortex, and less sensitive to graded levels of feature associations. The cortical activation of one ‘berry’ feature could then activate a subset of this conjunctive code in the hippocampus, which would then retrieve other features via pattern completion [8]. This representational structure would enable

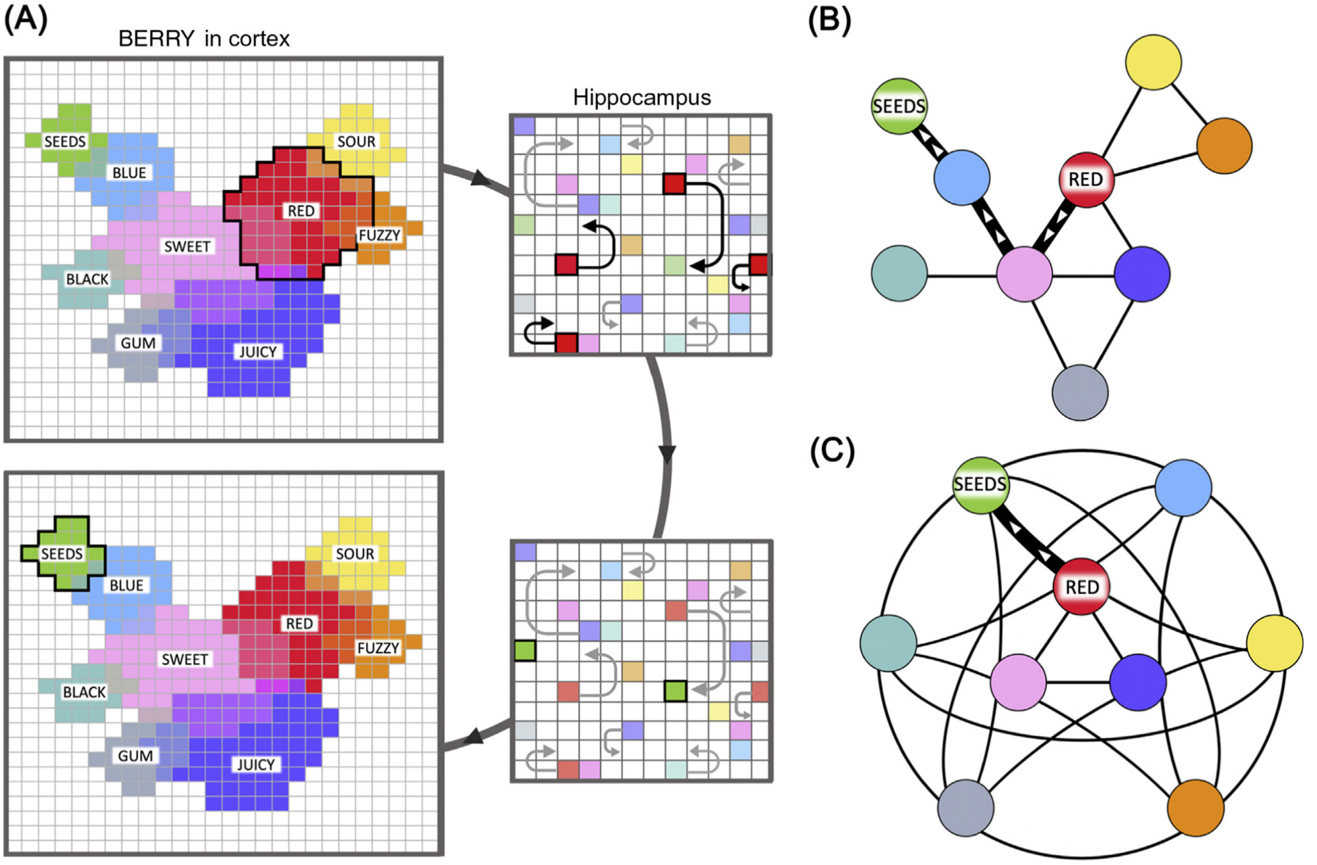

Figure 1. Cortical and Hippocampal Representations in Semantic Search. (A) The cortex has a representational code that reflects the rich co-occurrence structure of semantic features, in which some features are more central to a concept than others. Upon presentation of a semantic probe, the hippocampus reads in the full cortical semantic representation and forms a conjunctive representation of these features (as if they were features of an episode). This hippocampal representation loses the cortical spatial topography, and is less sensitive to the rich semantic structure stored in cortex, but allows pattern completion from one feature to any other within that concept through dense recurrent connectivity. The hippocampus can use this pattern completion process to move quickly to relatively distant features and then reinstate these more distant features in cortex. (B) The cortical concept network is structurally complex and contains large feature–feature distances. (C) The hippocampus creates a more fully connected network such that it is easier to traverse from one conceptual feature to another.

distant features to be more easily activated than if cortical representations alone were used. For example, healthy controls could use this hippocampal representation to access 'seeds' with relative ease (Figure 1C), whereas amnesics would be restricted to the complex cortical representation requiring longer traversals.

We propose that the hippocampus contributes a dynamically created conjunctive or relational code to semantic search, rather than a stored conceptual representation. This is consistent with the general notion that the hippocampus can contribute to remote memory retrieval in the absence of a stored hippocampal trace [3]. Although this is relatively uncontroversial for semantic memory, its tenability for episodic memory is still a matter of debate [9].

The existence of ‘concept cells’ in the hippocampus, which respond similarly to different instantiations of a given concept (e.g., ‘Jennifer Aniston’ [10]), could be taken as evidence that the hippocampus does store remote semantic memories. Another possible explanation for these findings, however, is that a concept cell is part of a hippocampal conjunctive code that is rapidly formed from cortical representations at the first presentation of a concept stimulus. That same conjunctive code then continues to be accessed throughout the experiment.

The mechanism of pattern completion over a dynamically formed conjunctive representation of cortical features may also explain the contribution of the hippocampus to other cognitive domains such as future thinking, perception, and working memory [1]. As CDP demonstrate, applying rich models to empirical data provides useful theoretical constraints.

Similar investigations of hippocampal function across domains are likely to be a fruitful direction for further empirical and modeling work.

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