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Expanding the language network: Direct contributions from the hippocampus

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Abstract

New research suggests that the same hippocampal computations used in support of memory are also used for language processing, providing direct neurophysiological evidence of a shared neural mechanism for memory and language. This work expands classic memory and language models and represents a new opportunity for studying the memory-language interface.

Keywords

hippocampus; theta oscillations; memory; language; online processing

Recordings of electrical activity from the hippocampus, and related structures, show a prominent amplitude oscillation termed theta rhythm (or theta oscillation) that is critical in memory function and in the timing of interactions between hippocampus and other brain regions [1]. Piai et al. recently reported the surprising finding that these hippocampal theta oscillations are also evident during sentence processing and are modulated by the amount of contextual linguistic information provided in sentences [2]. The observed hippocampal contribution to language processing was revealed by taking direct recordings from stereotactically implanted depth electrodes in patients (for localization of epileptic foci). These patients listened to sentences with the final word omitted and were then presented with a picture to name that could complete the sentence. In the experiment, half of the sentences presented to the patients began with a sentence stem that linguistically constrained the possible final word (e.g., “She locked the door with the” (picture: key)) while the other half were linguistically unconstrained (e.g., “She walked in here with the” (picture: key)). Increases in hippocampal theta oscillations were reported for constrained relative to unconstrained sentences. Not only were hippocampal theta oscillations observed during sentence processing, but theta power increased over the course of processing for constrained sentences relative to unconstrained sentences (i.e., hippocampal theta oscillations tracked the greater and increasing semantic associations among words in the constrained sentences as they unfolded). Although the hippocampus is not included in any prominent language

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models, these findings provide direct, real-time, neurophysiological evidence for ongoing hippocampal contributions to the online processing and use of language.

A growing literature suggests that the same cognitive and neural processes by which the hippocampus supports memory are among the same processes required for the effective operation of non-mnemonic cognitive abilities (see [3] for review). For example, there are numerous studies documenting a range of deficits and disruptions in language use in patients with hippocampal amnesia across linguistic domains and tasks (e.g. [4,5]). This work led to the proposal that the hippocampus, in its capacity for relational binding, representational integration, flexibility, and maintenance, is a critical contributor to meeting many of the demands of language use and processing [4]. The results by Piai and colleagues represent a significant extension of this idea by providing evidence of a shared neural mechanism for memory and language. But, what are the implications of this shared mechanism for understanding the instantiation of memory and language in the brain? We suggest, as a starting point, consideration of the behavioral demands/opportunities for which memory and language might draw on the same set of neural computations. We offer the example of predictive processing as one fruitful avenue for examining the language-memory interface in complex behavior.

The hippocampus has been linked to prediction and predictive processes [6,7]. Drawing on the same constructive processes associated with (re)combining and (re)instantiating the constituent elements of past episodic memory, the hippocampus supports the ability to simulate and predict future events. Notably, prediction also plays a crucial role in language processing. As language unfolds over time, we generate predictions about upcoming words, drawing on our long-term memory representations of individual words, patterns of lexical co-occurrence and syntactic probabilities, and the past and immediate discourse history. A recent fMRI study [8] reported hippocampal activation during a language prediction task, raising the possibility that the hippocampus may support language processes in the generation of a prediction or in the detection of a prediction error (i.e., by matching predicted sequences to the actual perceptual input). The ability to anticipate or predict the future has obvious evolutionary advantages and confers cognitive efficiency [9]. One possibility is that the hippocampus supports a domain-general capacity for predictive processing that is recruited in service of both episodic thinking and communication.

Piai and colleagues argue [1] that the increases in hippocampal theta-power observed in their study were associated with active, on-going relational processing of incoming words to previously acquired and stored semantic knowledge. Although this study is the first to relate hippocampal theta oscillations to language processing, in the memory literature theta oscillations are thought to link hippocampus and neocortex, providing a dynamic and distributed set of connections among memory representations [10]. An open question is whether hippocampal theta oscillations provide similar associative links between hippocampus and canonical language areas (e.g., perisylvian cortical regions). Furthermore, it remains to be determined if the observed hippocampal theta oscillations reported by Piai and colleagues extend to other aspects of language processing outside of semantics. In terms of shared neural mechanisms, we speculate theta oscillations likely represent the connection between the hippocampus and neocortical storage sites broadly and may reflect active,

ongoing processing for all manner of information and processing (i.e., for memory and for language).

Memory and language have long been studied in isolation and have been treated as distinct psychological constructs with distinct neural substrates. If memory and language share a common neural mechanism, how do we represent this overlap in our models of language and memory? The direct neurophysiological evidence of hippocampal contributions to language processing reported by Piai and colleagues, taken together with the behavioral data documenting disruptions in language use following hippocampal pathology ([4,5]) argue for the inclusion of the hippocampus as part of the language network. Continued work examining the nature and time course of hippocampal activity with the rest of the language network will provide greater precision in understanding its role as part of the network's core (i.e., those brain regions that coactivate with each other during a given task or type of processing) or periphery (i.e., those brain regions that may coactivate with a set of regions at some times but with other specialized systems at other times, depending on demands) [11]. Such work may also illuminate the range of shared, as well as specialized, neural mechanisms for memory and language. The recent work by Piai and colleagues offers a novel method for investigating the memory-language interface that serves to expand our understanding of the interdependencies and the neurobiology of our two most quintessential human abilities: memory and language.

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References

1. Hasselmo ME. What is the function of hippocampal theta rhythm? Linking behavioral data to phasic properties of field potential and unit recording data. *Hippocampus*. 2005; 15:936–949. [PubMed: 16158423]
2. Piai V, et al. Direct brain recordings reveal hippocampal rhythm underpinnings of language processing. *Proc. Natl. Acad. Sci.* 2016; 113:11366–11371. [PubMed: 27647880]
3. Rubin RD, et al. The role of the hippocampus in flexible cognition and social behavior. *Front Hum Neurosci.* 2014; 8:1–15. [PubMed: 24474914]
4. Duff MC, Brown-Schmidt S. The hippocampus and the flexible use and processing of language. *Front. Hum. Neurosci.* 2012; 6:1–11. [PubMed: 22279433]
5. MacKay DG, et al. H.M. revisited: Relations between language comprehension, memory, and the hippocampal system. *J. Cogn. Neurosci.* 1998; 10:377–394. [PubMed: 9869711]
6. Buckner RL. The role of the hippocampus in prediction and imagination. *Annu. Rev. Psychol.* 2010; 61:27–48. [PubMed: 19958178]
7. Mullally SL, Maguire EA. Memory, imagination, and predicting the future: A common brain mechanism? *Neurosci.* 2014; 20:220–234.
8. Bonhage CE, et al. Combined eye tracking and fMRI reveals neural basis of linguistic predictions during sentence comprehension. *Cortex.* 2015; 68:33–47. [PubMed: 26003489]
9. Clark A. Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav. Brain Sci.* 2013; 36:181–253. [PubMed: 23663408]
10. Watrous AJ, et al. Frequency-specific network connectivity increases underlie spatiotemporal memory retrieval. *Nat. Neurosci.* 2013; 16:349–356. [PubMed: 23354333]

11. Fedorenko E, Thompson-Schill S. Reworking the language network. *Trends Cogn. Sci.* 2014; 18:120–126. [PubMed: 24440115]