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The devil may be in the details: The need for contextually rich stimuli in memory consolidation research

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ABSTRACT

Systems consolidation theory (SCT) proposes that the hippocampus is not required for retrieval of remote memories. In this issue, Tallman and colleagues observe reduced hippocampal-cortical connectivity in recognition memory as a function of memory age, which they interpret as supportive of SCT. We suggest that research seeking to inform this debate would benefit from using perceptually rich stimuli that promote the recollection of high-fidelity contextual details. Tests of recognition alone may not be capable of discerning whether reductions in hippocampal activity or connectivity reflect remote memory retrieval independent of hippocampus (consistent with SCT) or a time-dependent decline in episodic detail.

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The extent to which the hippocampus is necessary for the retrieval of remote memories has long been debated. Two key theories are systems consolidation theory (SCT), which proposes that memories become increasingly independent of the hippocampus until they can be supported solely by neocortex (e.g., Alvarez & Squire, 1994), and multiple trace theory (MTT), which contends that the hippocampus is always required for the retrieval of contextually rich, episodic memories, establishing additional memory traces during subsequent retrieval and re-encoding, and strengthening neocortical connectivity and semantic representations of an experience (e.g., Moscovitch et al., 2005). In their study, Tallman and colleagues (this issue) contribute to this debate using functional neuroimaging and a clever design which boasts four time points for memory age, taking into consideration effects of reaction time, confidence ratings at retrieval and potential confounding effects of re-encoding.

Tallman et al.'s findings provide further support for changing dynamics between brain regions throughout the lifetime of declarative memories. Although hippocampal involvement was not reduced during retrieval of more remote memories, as SCT would predict, an observed decrease in hippocampal-neocortical connectivity with memory age was interpreted as evidence in support of SCT. Tallman and colleagues noted that the absence of a decrease in hippocampal activity over time does not preclude systems consolidation because the timeframe of the study may not have been sufficiently long to capture reduced hippocampal engagement.

There is also, perhaps, an additional explanation for the present results of reduced hippocampal-neocortical connectivity and for prior findings of decreased hippocampal activity as a function of memory age. It might be that reduced hippocampal activity and hippocampal-neocortical connectivity reflects a decline in the quality or episodic richness of remote memories. The findings presented by Tallman and colleagues remained even after controlling for the effect of memory confidence, used by them as a proxy of recollection. Moreover, in their review of previous work on memory consolidation the authors noted that a number of studies analyzing high-confidence hits and recollection-based trials demonstrated reduced hippocampal activity for remote memories, seemingly contradicting this possible alternative account of the data.

Under closer inspection though, an interesting pattern emerges from these investigations: studies using recognition memory tasks with low demands on contextual details (similar to methods employed by Tallman et al.) observed the expected decrease in hippocampal activity (Dandolo & Schwabe, 2018; Milton et al., 2011; Sterpenich et al., 2009; Takashima et al., 2006), whereas studies placing greater demands on contextual information observed stable hippocampal engagement during trials in which such detail was retained, coupled with reduced hippocampal activity when this was not the case (Harand et al., 2012; Ritchey et al., 2015). Moreover, in two studies requiring recall of episodic details from naturalistic stimuli (video clips), there were no differences in hippocampal activity during retrieval of recent and remote memories

when only trials characterized by recollection of high-fidelity mnemonic representations were considered (Furman et al., 2012; Sekeres et al., 2018). These findings may be more consistent with trace transformation theory, which builds on MTT and posits that the majority of memory representations are transformed to become more gist-like over time (which would explain a reduction in hippocampal activity for remote memories when averaging across all trials in a given experiment), while some memories retain their episodic richness into 'old age' (Gilboa & Moscovitch, 2021). This pattern of results in prior studies also casts new light on the finding of reduced hippocampal-neocortical connectivity observed by Tallman and colleagues: decreased crosstalk between these regions may reflect the reinstatement of memories with less episodic detail and reduced precision (Cooper & Ritchey, 2019). Without trial-wise information concerning the retrieval of detailed memory representations, it is difficult to rule out this alternative explanation of the present data. Even when controlling for confidence and classifying trials based on remember/know judgments, reinstatement of remote memories may on average be less episodically rich. In recognition memory paradigms such as those used by Tallman and colleagues, a 'remember' response in a hit trial may reflect the retrieval of a single diagnostic feature or the recollection of a stimulus in all of its episodic detail. Categorical responding to a single memory question cannot easily disambiguate these two scenarios.

How then should one seek to obtain evidence in favor of SCT or other accounts of memory consolidation in functional neuroimaging experiments? The devil may be in the details. Ideally, future work could use a design that includes stimuli rich in episodic detail, consider multiple time points as done in the present study, and classify trials based on whether contextual information was recalled. Continuous response measures that capture the precision or fidelity of retrieved memories may further aid in this endeavor. Under such conditions, findings consistent with systems consolidation would be a decline in hippocampal activity, coupled with a reduction in hippocampal-neocortical connectivity (particularly with prefrontal and lateral parietal regions) and an increase in cortico-cortical regional communication, which can even be observed during trials in which recollection of high-fidelity contextual details occurs.

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