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Hippocampal activity supporting working memory is contingent upon specific task demands

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ABSTRACT

Working memory (WM) is the ability to maintain and manipulate internal representations. WM recruits varying brain regions based on task demands. Although the hippocampus has historically been associated with long-term memory (LTM), several studies provide evidence for its involvement during WM tasks. Slotnick (this issue) posits that this involvement is due to LTM processes. This argument rests on the assumption that processes are not shared among WM and LTM, and that WM processes are necessarily sustained. We argue that there are processes utilized by both WM and LTM, and that such processes need not be sustained to support WM.

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A traditional view of memory systems is that they can be distinguished by the timescales over which they operate (e.g., Atkinson and Shiffrin (1968)). Classic evidence for this view shows that damage to the hippocampus leaves recent memories intact, while severely impairing memory for information presented further into the past (e.g., Scoville and Milner (1957)). Such data support a separation between a hippocampal-dependent LTM from non-hippocampal-dependent systems that act over shorter timescales, such as WM.

With advancements in neuroimaging, hippocampal involvement was discovered in WM tasks (e.g., Ranganath and D'Esposito (2001)). Such data were bolstered by findings that patients with hippocampal damage demonstrated impairments when WM tasks involved novel stimuli (Ranganath & Blumenfeld, 2005) or probed item-context associations (Hannula et al., 2006; Olson, 2006; Olson et al., 2006). This suggests that hippocampal involvement is not about time per se, but rather about demands to create novel associations (Ranganath, 2006). Such demands are essential to LTM, but particular to WM tasks that employ this function.

Slotnick (this issue) challenges this view arguing that hippocampal involvement in WM tasks is attributable to LTM processes. According to Slotnick (this issue), hippocampal activity can only be unambiguously associated to WM during late delay periods of maintenance intervals. He assumes that encoding, early delays, and retrieval periods reflect some contribution of LTM processes such that respective hippocampal activity reflects LTM

rather than WM. Therefore, he concludes that there is no evidence of hippocampal involvement in WM.

One of Slotnick's (this issue) fundamental assumptions is that if a process is involved in LTM, that belies its necessity for WM. However, this precludes the possibility that some processes are necessary for both LTM and WM. For example, damage to sensory systems would impair both WM and LTM for the information processed by such systems. Thus, when Slotnick (this issue) assumes that the involvement of a brain system during encoding can be attributable to LTM processes, he assigns processes that could potentially facilitate both short- and long-term retention solely to one system.

If the hippocampus supports forming novel associations, this function may aid both LTM and WM, but only in cases where associational information is tested. It is notable that LTM tasks testing recognition do not require the hippocampus (Yonelinas et al., 2002). Similarly, most WM tasks use familiar stimuli requiring recognition memory. Such tasks would not be expected to require the hippocampus. Alternatively, tasks testing the ability to associate familiar items to contexts have been shown to rely on the hippocampus in both the long-term (Davachi, 2006; Eichenbaum et al., 2007) and short-term (Hannula et al., 2006; Olson, 2006; Olson et al., 2006). Thus, the hippocampus serves a function that can support both LTM and WM when demands require novel associations or be unnecessary when demands do not.

A second assumption that Slotnick (this issue) makes is that neural activity supporting WM is necessarily

sustained over time. While this assumption follows from traditional views of WM maintenance (e.g., D'Esposito (2007)), more contemporary views recognize that sustained activity need not be necessary for WM maintenance (e.g., Miller et al. (2018); Stokes (2015)). Indeed, sustained activity may only occur for specific task demands (Orhan & Ma, 2019). In the absence of sustained activity, other mechanisms may support the retention of information in the short-term that cannot be overtly measured by the BOLD signal (e.g., Mongillo et al. (2008)). Hence, the assumption that only activation that persists into the late delay can be unambiguously assigned to WM is faulty. Moreover, any activation that does persist into the late delay may or may not directly reflect maintenance processes as opposed to other processes that may persist over retention intervals (e.g., vigilance). Finally, sustained activation need not be maintained at the same levels throughout a retention interval. Numerous findings support the idea that neural activity supporting WM can be highly dynamic (e.g., Brody et al. (2003), Romo and Salinas (2001), and Stokes (2015)). Additionally, any design that can distinguish late from early delay intervals relying on the BOLD signal requires lengthy delay periods over which memory may degrade (Brown, 1958; Peterson & Peterson, 1959). Activation reflecting the representation of such memories may degrade accordingly. Collectively, the assumption that the late delay is the critical period to isolate WM is problematic.

As reviewed by Slotnick (this issue), several studies testing WM report hippocampal activations, particularly those requiring novel associations. We contest that late delay maintenance activations should not be the gold standard against which the necessity of hippocampal involvement in WM should be measured against. Rather, hippocampal-dependent processes supporting WM may occur at various times depending upon task demands.

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