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Hippocampal involvement in working memory following refreshing

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ABSTRACT

Working memory (WM) and long-term memory (LTM) tests have both overlapping and distinct neurocognitive processes. Hippocampal activity in fMRI studies–a hallmark of LTM–also occurs on WM tasks, typically during encoding or retrieval and sometimes (albeit rarely) through 'late-delay' periods. The Synaptic Theory of WM suggests that 'activity-silent' synaptic weights retain temporary, WM-relevant codes without sustained, elevated activity. The hippocampus temporarily retains item-context bindings during WM-delays that are typically 'silent' to fMRI, probably via oscillatory patterns of informational connectivity among task-relevant regions of cortex. Advancing WM theory will require modeling this dynamic interplay, as in the 'Dynamic Processing Model of WM.

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The question of how short-term or working memory (WM) is distinguished from long-term memory (LTM) has been central to memory research from its beginning.[1] In this issue, Slotnick's review and meta-analysis of fMRI studies showing hippocampal activity during WM tasks stated that WM processes can only be distinguished from LTM processes during the 'late' delay period of a WM task.[2] Tests of WM and LTM share many neurocognitive processes (including hippocampal activity), especially during encoding/early-delay and retrieval phases of WM tasks. Ascribing such activation to only LTM requires clarification, however.

From an emergent/embedded processing view (Cowan, 1999; Postle, 2006), information is encoded as the products of perceptual, attentive, and cognitive processing, whose nature varies according to one's goal. If fewer than ~7 bits (Miller, 1956) or ~3 chunks (Cowan, 2001, 2015) of information is to be briefly maintained in mind, as in most WM tasks, then one tends to engage in shallower, perceptual/rehearsal-based, levels-of-processing (LOP; Craik & Jacoby, 1975; Speer et al., 2003), so hippocampal activity is unlikely. If material is to be remembered after longer (filled) delays, as in most LTM tests, then one tends to engage in deeper, conceptual/elaborative LOP–but this also happens on WM tasks (depending on the context, e.g., test expectations, delay interference; Rose et al., 2014; Rose & Craik, 2012; Rose et al., 2010). For example, Rose et al. (2015) had young adults answer a deep ('Is living?') or shallow ('Contains an "e"?') question about a single word (moose) that was to be recalled after 10 seconds of either rehearsal, easy-math, or hard-math on each trial. Slotnick concluded that this study does not inform the debate about whether and how LTM is involved in WM because recall following the math conditions was 'confounded' by retrieval from LTM. But this is not a confound–the experiment manipulated the involvement of LTM/hippocampal-activity in recall of one word following either continuous rehearsal, easy-math (which some theorists hypothesize to involve refreshing–a maintenance mechanism presumed to be distinct from both rehearsal and LTM retrieval, Camos, 2015; Raye et al., 2007), and hard-math (which most theorists hypothesize to involve LTM retrieval, Cowan, 2008; Jonides et al., 2008).

Rose et al. found that hippocampal activity was involved and predicted successful recall in both the easy- and hard-math conditions, which suggests that recalling a single word after brief distraction involved LTM episodic retrieval processes, even when maintaining the word was assumed to involve 'refreshing.'

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[1]Note that Slotnick (like many others) conflated short-term memory (STM) with WM. According to many cognitive and neuroscientific theories, hippocampal/LTM processes are less likely to be involved in STM tasks associated with continuous, active maintenance of information in focal attention than in WM tasks associated with noncontinuous maintenance (i.e., refreshing) during the processing/manipulation of information in the presence of interference/distraction (Cowan, 2008; D'Esposito & Postle, 2015; Jonides et al., 2008; Oberauer et al., 2018). This distinction is critical for interpreting hippocampal/LTM processes during STM or WM tasks.

[2]Note that the time range that constitutes a 'late' delay period was not specified. Based on a substantial amount of research on the effects of interference/distraction on WM irrespective of time/delay, many researchers believe that time is not the critical factor that determines whether something is actively retained in and reported 'from WM' or is dropped from active maintenance and must be retrieved 'from LTM' using episodic retrieval processes (Cabeza et al., 2002; Cowan, 2008; Rose & Craik, 2012; Rose et al., 2010; Foster et al., (in press)). This distinction is also critical for interpreting hippocampal/LTM processes during WM tasks.

Consistent with Slotnick's claim, hippocampal activity was not involved following rehearsal. We interpreted this to mean that refreshing is similar to LTM/episodic retrieval (see also, Rose et al., 2014). The point is that the type of neural code that is maintained in WM, and the extent to which the hippocampus is involved, changes when sustained, active-maintenance (rehearsal) mechanisms are disrupted.

If hippocampal activity is not sustained through a WM delay period, how might its neural computations support WM retention? A major function of WM is to resolve the proactive interference when trying to remember whether items in mind are either currently- or previously-relevant. This likely happens through the binding of item-context associations via the hippocampus during perception/encoding irrespective of the task (Olsen et al., 2012; Yonelinas, 2013). According to many models, such item-context bindings are only temporarily retained (e.g., in the focus of attention) and are removed/deleted from WM when their maintenance is no longer relevant for ongoing cognition (Oberauer, 2019; Postle & Oberauer, in press). That is, they are actively maintained in and deleted from WM–not LTM. How might such bindings be retained without hippocampal involvement?

The Synaptic Theory of WM suggests that such temporary bindings may be represented in the pattern of synaptic weights among the network of neurons that represent information in WM (e.g., about a color and its location) while it is relevant for ongoing cognition; then these 'activity silent' short-term, synaptic-plasticity mechanisms are quickly dissolved when the information is no longer needed[3] (for reviews see, Beukers et al., 2021; Buchsbaum & D'Esposito, 2019; D'Esposito & Postle, 2015; Stokes, 2015). Rose et al. (2016) showed causal evidence for this theory using transcranial magnetic stimulation (TMS) applied to the precuneus (a key hub in the hippocampal network). The TMS-induced reactivation of 'activity silent' WM likely involved the propagation to, and activation of, the hippocampus (Nilakantan et al., 2017; Tambini et al., 2018). This has yet been confirmed for single-pulse TMS during WM delay periods with simultaneous neuroimaging, but see, Hermiller et al. (2020) for consistent evidence from theta-burst TMS during fMRI.

We suggest that LTM processes–including hippocampal activity–are recruited during WM tasks, typically during encoding or retrieval, and sometimes through the delay (Kumar et al., 2016; Olsen et al., 2009). This likely happens via connectivity with the fronto-parietal cortex, but in a dynamic, context-dependent manner (Rose, 2020). Understanding and modeling these dynamics is essential for advancing theory.

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[3]One complication with addressing this hypothesis is that it is difficult to test with fMRI or EEG alone. Slotnick (this issue) exclusively considered fMRI data. Other methods with greater temporal and spatial resolution, such as MEG or invasive recordings from within the hippocampus (single-unit or local-field potentials), may be necessary to detect 'silent' activity dynamics. For example, there is evidence that stimulus-specific, delay-period activity of 'concept' cells in the hippocampus retains information in WM through synchronized oscillatory dynamics (theta–alpha coupling) with prefrontal regions (Kamiński & Rutishauser, 2020; Kornblith et al., 2017), and this activity predicts WM load and accuracy (Boran et al., 2019; Kornblith et al., 2017).

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