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COMMENTARY

The hippocampus and implicit memory (by any other name)

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ABSTRACT

Is the hippocampus involved in implicit memory? I argue that contemporary views on hippocampal function, going beyond the classic dichotomy of explicit versus implicit, predict involvement of the hippocampus whenever flexible, predictive associations are rapidly encoded. This involvement is independent of conscious awareness. A paradigm case is statistical learning: the unconscious extraction of statistical regularities from the environment. In line with this, a substantial body of literature on contextual cueing in visual search has established hippocampal involvement in this form of implicit learning. To conclude, implicit memory (as such or by any other name) is associated with the hippocampus.

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Main text

In their provocative review, Steinkrauss and Slotnick (2024) identify 13 articles that link hippocampal activity to implicit memory, proceed to identify various confounds in each of them, and conclude that implicit memory is not associated with the hippocampus. Their reasoning may, with some imagination, be considered the meta-analytical equivalent of the imbalance confound they so rightly warn us against. Although some discussion is devoted to lesion studies, the systematic review is limited to fMRI studies only. More importantly, it is limited to studies mentioning ‘implicit memory’ explicitly. I will start by highlighting several strands of evidence that this limited query will have missed, and then point out how a contemporary interpretation of hippocampal function may alleviate any remaining confusion.

There is a large body of work related to the neural underpinnings of contextual cueing (Chun & Jiang, 1998; Goujon et al., 2015), a hallmark finding of implicit learning. Briefly, participants visually search for a rotated T amongst L-shaped distractors, and report the T’s orientation. Unbeknownst to the participants, some displays have repeated spatial configurations. These repeated (‘Old’) displays lead to enhanced performance, compared to random (‘New’) displays, indicating that learning of spatial configurations takes place. Participants are typically unable to explicitly distinguish Old from New displays in a surprise posttest, suggesting that the learning was implicit. To their credit, Steinkrauss & Slotnick discuss this phenomenon briefly in their Discussion, before dismissing it as not reflecting implicit learning (or involving the hippocampus proper). Their dismissal is based on a very slim number of studies reviewed, and I will attempt to rectify this by describing several further studies of high relevance.

First, sticking to the fMRI world, at least two studies report clear hippocampal involvement during contextual cueing, with reduced BOLD activity for Old displays, compared to New (Giesbrecht et al., 2013; Greene et al., 2007). Furthermore, this hippocampal effect was predictive of the later reaction time benefit. In both studies, there was no explicit recognition of Old versus New displays, indicating an implicit effect.

Second, evidence from magneto-encephalography (MEG) has implicated the hippocampal theta rhythm in contextual cueing (Spaak & de Lange, 2020), specifically during the learning phase. This study also sheds light on the implicit nature of the knowledge acquired. After the main search task, participants were debriefed about whether or not they felt that they recognized repeated displays. Following this, all participants performed the typical objective recognition test (Old versus New displays). This allowed the authors to examine the contextual cueing effect as a function of any explicit memory formed. Participants who reported a feeling of recognition were indeed objectively able to identify Old versus New displays above chance level, apparently validating Steinkrauss & Slotnick’s worry that contextual cueing is sometimes accompanied by explicit memory. However, crucially, these ‘recognizers’ showed

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a *weaker* contextual cueing effect (i.e., search task benefit) than the non-recognizers. Furthermore, explicit recognition performance was not associated with the hippocampal theta rhythm, while the contextual cueing effect was. It seems justified to conclude that contextual cueing, and the related hippocampal involvement, are indeed implicit.

So why were these studies missed by Steinkrauss & Slotnick? The latter study (Spaak & de Lange, 2020) was based on MEG, ruling it out by their focus on fMRI. More interestingly, the former two studies (Giesbrecht et al., 2013; Greene et al., 2007) involved fMRI, but did not mention 'implicit memory' anywhere in their abstract or title. Instead, the relevant type of memory may be signaled by terms like 'implicitly learned context,' 'without awareness,' or, critically, 'statistical learning.' Indeed, contextual cueing is considered a form of statistical learning (Goujon et al., 2015), which, by definition, is an unconscious process (Turk-Browne, 2012) in which the brain extracts regularities from the environment.

The neural basis of statistical learning is an active field of study, and one key finding is that it depends on the medial temporal lobe in general (Schapiro et al., 2014) and, specifically, on the hippocampus proper (Covington et al., 2018). This meshes well with a modern taxonomy of memory and learning that goes beyond the classic dichotomy of explicit versus implicit, and is instead based on a 'processing-based division' (Henke, 2010). According to this view, the hippocampus is involved in the rapid encoding of flexible (predictive) associations, independently of whether these involve conscious awareness or not (Buzsáki & Tingley, 2018; Stachenfeld et al., 2017).

Is the hippocampus involved in implicit memory? By adopting the only sensible definition of 'implicit memory' – learning which takes place independently of conscious awareness of what is learned – we see that it encompasses phenomena like statistical learning and the (unconscious) formation of predictive maps. Evidence for hippocampal involvement here is abundant, so the answer appears a clear 'yes.'

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