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Activity reductions in perirhinal cortex predict conceptual priming and familiarity-based recognition

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ABSTRACT

Although it is well established that regions in the medial temporal lobes are critical for explicit memory, recent work has suggested that one medial temporal lobe subregion – the perirhinal cortex (PRC) – may also support conceptual priming, a form of implicit memory. Here, we sought to investigate whether activity reductions in PRC, previously linked to familiarity-based recognition, might also support conceptual implicit memory retrieval. Using a free association priming task, the current study tested the prediction that PRC indexes conceptual priming independent of contributions from perceptual and response repetition. Participants first completed an incidental semantic encoding task outside of the MRI scanner. Next, they were scanned during performance of a free association priming task, followed by a recognition memory test. Results indicated successful conceptual priming was associated with decreased PRC activity, and that an overlapping region within the PRC also exhibited activity reductions that covaried with familiarity during the recognition memory test. Our results demonstrate that the PRC contributes to both conceptual priming and familiarity-based recognition, which may reflect a common role of this region in implicit and explicit memory retrieval.

1. Introduction

Conceptual implicit memory reflects the process by which associative or semantic cues prime the automatic retrieval of recently encountered information without any intentional recollection of the study event (Roediger & McDermott, 1993; Schacter, 1987). What differentiates conceptual implicit memory from other forms of implicit memory is that it is an enhancement in the speed or fluency of the processing of an item based on prior processing of its conceptual features. Whereas perceptual priming often requires a partial or complete re-instantiation of the studied stimulus (e.g., study *octopus*; complete word fragment *o-t-pu*-at test), conceptual priming can instead be elicited by simply providing a conceptually-related cue to a previously studied target, such as in free association priming (e.g., study *dolphin*; generate associate of *porpoise* at test). Elucidating the neural underpinnings of conceptual priming has been the focus of considerable work over the past decade.

In most behavioral studies, conceptual implicit memory tasks rely on the generation of studied items based on conceptual cues, but most fMRI studies have used conceptual *repetition* priming tasks in which semantic judgments (e.g., is *turtle* bigger than a shoebox) are performed on repeated (e.g., *turtle*) and unstudied (i.e., baseline) items. In these paradigms, behavioral priming manifests in the form of faster reaction times for repeated semantic judgments on studied items relative to semantic judgments on baseline items. Some fMRI studies have found that activity in perirhinal cortex (PRC) – a region within the medial temporal lobes (MTL) – is reduced during performance of repeated semantic decisions relative to novel semantic decisions (Heusser, Awipi, & Davachi, 2013; O'Kane, Insler, & Wagner, 2005; Voss, Hauner, & Paller, 2009; Voss, Federmeier, & Paller, 2012), suggesting the possibility that PRC may be involved in conceptual priming (for a review, see Dew & Cabeza, 2011).

However, whether repetition-related deactivations observed in these studies reflect conceptual priming per se, remains unclear. Priming for repeated semantic judgments can reflect fluent conceptual processing, but can also be influenced by response and perceptual repetition. It has in fact been proposed that activity reductions elicited during repeated semantic judgments (i.e., neural priming) may index response priming rather than conceptual priming (for a review, see Schacter, Dobbins, & Schnyer, 2004). For example, reversing semantic decisions for studied items, but not changing the semantic dimension that is being queried (e.g., is *turtle* smaller than a shoebox), disrupts behavioral and neural priming relative to repeated semantic decisions,

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indicating that these effects may reflect facilitated retrieval of stimulus–response associations, rather than concepts (Dobbins, Schnyer, Verfaellie, & Schacter, 2004; Horner & Henson, 2008). Furthermore, recent work has also observed neural priming in PRC to perceptual repetitions (e.g., Greene & Soto, 2012; for a review, see Ranganath & Ritchey, 2012), and more broadly, the PRC is considered to play an important role in perceptual processing (for reviews, see Bussey & Saksida, 2007; Graham, Barense, & Lee, 2010; Murray & Richmond, 2001). Accordingly, to clearly demonstrate a role for PRC in conceptual implicit retrieval, it is critical to measure conceptual priming separately from any response and perceptual repetition.

One recent study reported direct evidence for PRC involvement in conceptual priming without perceptual and response repetition (Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010). In that study, participants studied items (e.g., *squid*) and then at time of test were required to generate exemplars of various different categories (e.g., *sea creatures*). Relative to both age-matched controls and amnesic patients with relatively selective hippocampal damage, amnesic patients with damage that included PRC were significantly impaired on this task (i.e., they were no more likely to produce studied than nonstudied items). A parallel fMRI experiment in healthy young adults revealed that PRC activation was higher during encoding of words that were subsequently produced on the exemplar generation test (i.e., 'subsequently primed' items) than during encoding of words that were not produced on the priming test (i.e., 'subsequently unprimed' items). Furthermore, across participants, the magnitude of this subsequent priming effect correlated with behavioral measures of conceptual priming. This experiment revealed that PRC activity during initial encoding is critical for later conceptual implicit memory, but does not indicate whether the PRC is sensitive to conceptual priming during retrieval. That is, it is possible that the PRC may be involved in the initial elaborative processing that is necessary for conceptual priming to occur, but it may not be involved in the process of retrieval.

Although interest in the contribution of PRC to conceptual implicit memory has emerged recently, a large body of work has implicated the PRC in explicit memory retrieval, and in particular, familiarity-based recognition (for reviews, see Brown & Aggleton, 2001; Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007). Familiarity reflects item retrieval based on acontextual memory strength—in contrast to recollection, which reflects the qualitative retrieval of context or source information (for a review, see Yonelinas, 2002). There is evidence that damage to PRC selectively impairs familiarity-based recognition (Bowles et al., 2007), and consistent with the conceptual repetition priming studies described above, numerous studies have shown that PRC exhibits repetition-related deactivations during recognition memory retrieval. The presentation of studied items at test – compared to unstudied items – is often accompanied by reductions in PRC activity (e.g., Henson, Cansino, Herron, Robb, & Rugg, 2003; Brozinsky, Yonelinas, Kroll, & Ranganath, 2005; for a review, see Wais, 2008), and furthermore, it has also been demonstrated that increases in the familiarity, or memory strength, of items during recognition tests is related to decreases in PRC activity (e.g., Daselaar, Fleck, & Cabeza, 2006; Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Montaldi, Spencer, Roberts, & Mayes, 2006; but see Yonelinas, Otten, Shaw, & Rugg, 2005). Based on this literature, PRC deactivations during recognition tasks have been interpreted to reflect fluent processing of previously studied items that supports familiarity-based recognition discriminations (Fernandez & Tendolkar, 2006). This is in contrast to the hippocampus, which is thought to be critical for recollection-based recognition, but unnecessary for both familiarity-based recognition and conceptual priming (for reviews, see Dew & Cabeza, 2011; Ranganath & Ritchey, 2012).

Given that activity reductions are observed in PRC during both conceptual repetition priming and familiarity-based recognition judgments, it is possible that the same PRC-mediated process facilitates both conceptual implicit memory and familiarity-based recognition. Both forms of memory are sensitive to many of the same behavioral manipulations (for reviews, see Henke, 2010; Yonelinas, 2002), and direct comparisons across participants has indicated that familiarity and conceptual implicit memory are correlated (Wang & Yonelinas, 2012b). However, evidence from fMRI studies that have directly compared recognition and conceptual implicit memory is more mixed. Some did not report PRC involvement in either retrieval task (Donaldson, Petersen, & Buckner, 2001; Voss, Reber, Mesulam, Parrish, & Paller, 2008), and one other study observed activity reductions in PRC related to conceptual repetition priming, but none related to familiarity-based recognition (Voss et al., 2012).

Here, we sought to determine if the PRC was involved in supporting conceptual implicit memory at the time of retrieval, and to clarify the role of PRC in supporting both conceptual priming and familiarity-based recognition. As schematized in Fig. 1A, at study, participants incidentally encoded a list of words, half of which served as studied items in the subsequent free association priming task, and the other half served as studied items in the subsequent recognition memory test. Following encoding, participants first completed the free association task in the MRI scanner where they were presented with a series of word cues and asked to respond with the first word that came to mind for each cue. Unbeknownst to participants, some of the cues were selected to be semantically associated with previously studied words. This allowed us to examine PRC activity in the instances when they were conceptually primed to produce a previously studied word. We expected that, if PRC indexes conceptual priming, activity should be decreased on trials that were associated with successful priming (i.e., generation of a studied target in response to an associated cue), relative to both unprimed (i.e., when an associated cue did not prime the generation of a studied target) and baseline (i.e., cues that were unrelated to studied items) trials. Following the free association priming task, we also examined recognition memory confidence and aimed to determine whether PRC would show evidence for decreased activity as a function of recognition confidence. Anatomical region of interest (ROI) and voxel-based analyses of the PRC were conducted for both retrieval tasks, the former of which provided more

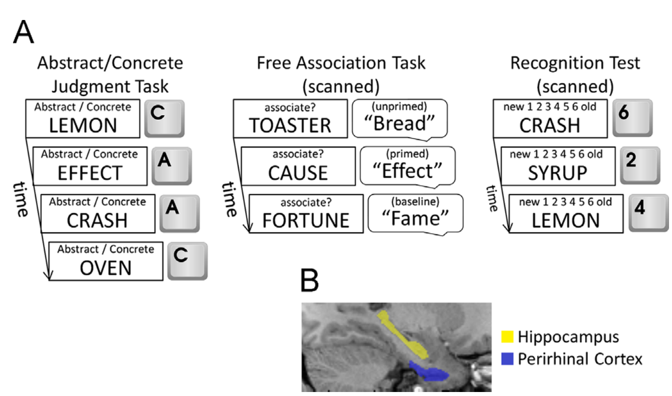

Fig. 1. Experimental procedure and ROI tracings. (A) Schematic depiction of the experimental procedure. Participants first incidentally encoded words by completing an abstract/concrete judgment task. Half of these words served as studied targets in a subsequent scanned free association task and the other half served as studied words in a subsequent scanned recognition memory test. (B) Example of individually-defined ROI tracings of PRC and hippocampus from a representative participant.