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# Elucidating the neural correlates of related false memories using a systematic measure of perceptual relatedness

Indira C. Turney*, Nancy A. Dennis

*The Department of Psychology, The Pennsylvania State University, 450 Moore Building, University Park, PA 16802, USA*

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ABSTRACT

Previous memory research has exploited the perceptual similarities between lures and targets in order to evoke false memories. Nevertheless, while some studies have attempted to use lures that are objectively more similar than others, no study has systematically controlled for perceptual overlap between target and lure items and its role in accounting for false alarm rates or the neural processes underlying such perceptual false memories. The current study looked to fill this gap in the literature by using a face-morphing program to systematically control for the amount of perceptual overlap between lures and targets. Our results converge with previous studies in finding a pattern of differences between true and false memories. Most importantly, expanding upon this work, parametric analyses showed false memory activity increases with respect to the similarity between lures and targets within bilateral middle temporal gyri and right medial prefrontal cortex (mPFC). Moreover, this pattern of activation was unique to false memories and could not be accounted for by relatedness alone. Connectivity analyses further find that activity in the mPFC and left middle temporal gyrus co-vary, suggestive of gist-based monitoring within the context of false memories. Interestingly, neither the MTL nor the fusiform face area exhibited modulation as a function of target-lure relatedness. Overall, these results provide insight into the processes underlying false memories and further enhance our understanding of the role perceptual similarity plays in supporting false memories.



## Introduction

The ability to accurately remember previous experiences and differentiate between previously encountered information and new information is critical to maintaining accurate memory. However, several factors make this distinction difficult, including the amount of perceptual similarity shared between old and new information. In the field of memory, the inaccurate identification of a new item, irrespective of its similarity to a studied item, is known as a false memory. In the domain of false memories, perceptual overlap between targets and lures has shown to result in an increased rate of false memories through the influence of gist-based processes (i.e., memory for general features of an episodic event) (Garoff-Eaton et al., 2006; Gutchess and Schacter, 2012; Slotnick and Schacter, 2004; Stark et al., 2010). While perceptual false memories have been widely studied in the literature, research has only taken a cursory investigation into the role of perceptual overlap between lures and targets in false memories. Specifically, previous false memory studies have not systematically controlled how the specific degree of perceptual overlap between lures and targets influences the neural mechanisms underlying false memories. To address this issue, the current study aimed to expand upon previous perceptual false memory studies by systematically varying the degree of perceptual relatedness between lures and targets.

One prominent theory of false memories, the Fuzzy Trace Theory, suggests false memory errors result as a consequence of an overreliance on gist traces of the encoding event at the expense of a reliance on item-specific details from encoding at the time of memory retrieval (Brainerd and Reyna, 1990). Furthermore, the amount of false memories to lure items is suggested to be a function of the amount of perceptual similarity or gist overlap between targets and lures. Previous research suggests that the sharing of gist traces between targets and lures is a critical factor in accounting for the rate of false memories (e.g., Gutchess and Schacter, 2012; Koutstaal and Schacter, 1997; Roediger and Mcdermott, 1995). Specifically, individuals make more false alarms to lures that share perceptual properties (i.e., via shape or color) with targets than to items that do not. Yet, prior neuroimaging studies have failed to systematically control for the degree of perceptual overlap or relatedness between targets and lures (but see Gutchess and Schacter (2012) for parametric increases in gist

* Corresponding author.
*E-mail addresses:* ict105@psu.edu (I.C. Turney), nad12@psu.edu (N.A. Dennis).

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encoding).

In general, perceptual false memory paradigms exploit the perceptual overlap in features between target and lure items to induce false memories (e.g., Gutchess and Schacter, 2012; Koutstaal and Schacter, 1997; Slotnick and Schacter, 2004). Specifically, participants are presented with pictures of one or more exemplars from various categories during encoding (e.g., 'chair'; 'dog'). During retrieval target items are intermixed with related lures (category exemplars that were not presented at encoding) and unrelated lures (new items whose category was not presented during encoding, e.g., Dennis et al., 2012; Koutstaal and Schacter, 1997; Slotnick and Schacter, 2004). False alarm rates to such related lures often mirror or closely approximate hit rates to target items. That is, perceptually related lures are likely to be classified as "old" at a similar rate as targets (Glanzer and Adams, 1985; Hockley, 2008; Nosofsky et al., 2011) as participants have difficulty in distinguishing between the two related items, while unrelated lures are relatively easily rejected. While some studies have attempted to use lures that are objectively more similar than others (Bowman and Dennis, 2016), no study has systematically controlled for the degree of perceptual overlap between targets and lures in order to investigate the influence of perceptual similarity on false memories.

Coinciding with this behavioral findings, neuroimaging studies examining perceptual based false memories have found differences in neural activation supporting true and false memories (for review, see Dennis et al. (2015)). For example, studies have shown that perceptual false memory retrieval in which there was a shared semantic component (e.g., similar category membership between targets and lures) and shared perceptual features, rely on processing within left middle and superior temporal gyri and late visual cortices (e.g., Dennis et al., 2012; Garoff-Eaton et al., 2006; Slotnick and Schacter, 2004). Researchers have interpreted this activation as evidence of an overreliance on perceptual gist and general processing of object identity supporting memory retrieval. Furthermore, as increased activation in lateral temporal cortex is also found to support false compared to true memories, researchers have suggested it reflects increased reliance on gist information, in the absence of a detailed or item-based retrieval signal (for review, see Dennis et al. (2015)).

Activity in the prefrontal cortex (PFC) has also been shown to differentiate between false memories to perceptually related lures and true memories (Cabeza et al., 2001; Garoff-Eaton et al., 2007; Kensinger and Schacter, 2006; Kim and Cabeza, 2007b; Kubota et al., 2006; Okado and Stark, 2003; Schacter et al., 1996). Studies have attributed this increased PFC activity to an increased need for monitoring, reconstructive processes, and semantic elaboration supporting false memories—with the specific interpretation dependent upon the precise locus of PFC activation. A recent meta-analysis found the most consistently activated frontal region underlying false memories is the medial PFC (mPFC) (Kurkela and Dennis, 2016), which has been associated with greater reliance on retrieval monitoring and evaluation processes necessary when making difficult memory decisions related to critical lures (e.g., Hofer et al., 2007; Iidaka et al., 2012).

Another notable difference between true and false retrieval is the finding of increased activity in early visual processing regions (i.e., BA 17 & 18) for true compared to false memories. This has been interpreted within the context of the '*sensory reactivation hypothesis,*' (e.g., Marche et al., 2010; Mather et al., 1997; Norman and Schacter, 1997). Specifically, the sensory reactivation hypothesis postulates that, by virtue of having been presented previously, target items will elicit retrieval-related reactivation of the encoding episode in sensory regions that were involved in their initial encoding (e.g., Vaidya et al., 2002; Wheeler et al., 2000). This is in contrast to related lures, which on the other hand, were not previously presented and thus are not accompanied by this heightened sensory signal at retrieval. However, despite strong evidence supporting the sensory reactivation hypothesis, not all perceptual false memory studies find this dissociation (e.g., Garoff-Eaton et al., 2006; Gutchess and Schacter, 2012). For example, using categorized pictures, Gutchess and Schacter (2012) found that false memories associated with a stronger semantic gist representation (which was manipulated by presenting groupings of either 4, 8, or 14 exemplars per category of stimuli at encoding), resulted in increased activation in both the hippocampus and visual processing regions (BA 17 and 37). One explanation for this difference across studies may be related to the properties of the lure stimuli in relation to the target stimuli. That is, perhaps when related lures and targets share significant perceptual overlap with one another, the presentation of the lure at retrieval is sufficient to reactivate the perceptual experience from encoding (Gutchess and Schacter, 2012), compared to when they share less overlap. However, no study has investigated this by systematically controlling for the perceptual similarity between targets and lures.

Further still, another region that has shown varied findings with respect to distinguishing true and false memories is the medial temporal lobe (MTL). While some studies have found the hippocampus/parahippocampal gyrus (PHG) to support both true and false retrieval (e.g., Dennis et al., 2012; Garoff-Eaton et al., 2006; Gutchess and Schacter, 2012; Kahn et al., 2004; Slotnick and Schacter, 2004; Stark et al., 2010; von Zerssen et al., 2001), others find greater MTL involvement associated with true compared to false memories (e.g., Cabeza et al., 2001; Dennis et al., 2012', 2008b; Giovanello et al., 2009; Kahn et al., 2004; Kensinger and Schacter, 2006; Kim and Cabeza, 2007b; Paz-Alonso et al., 2008). Studies suggest that greater MTL activation for true memories reflects greater recovery of sensory details associated with targets (Cabeza et al., 2001; Kahn et al., 2004; Okado and Stark, 2003), while others suggested this neural increase reflects the role of the hippocampus in binding together true details from past events (Kensinger and Schacter, 2006), or recollection processes (Dennis et al., 2012; Kim and Cabeza, 2007b). Interestingly, despite the foregoing findings, a recent meta-analysis found no consistent role for the MTL in supporting false memories (for review, see Kurkela and Dennis (2016)).

Such varied results may reflect several factors including methodological differences across studies and/or the measured degree of overlap between the related lure and the target item from the same category. With respect to item relatedness, research shows that the anterior portions of the MTL track relatedness (Bowman and Dennis, 2015; Daselaar et al., 2006; Kirchhoff et al., 2000; Tulving et al., 1996) and reflects bottom-up novelty signals, triggered by less related items. Furthermore, researchers posit that this increase in activation reflects a mismatch or recall-to-reject signal within the MTL (Bowman and Dennis, 2015; Kumaran and Maguire, 2009), beyond that found for item novelty alone (Brown and Aggleton, 2001) or unrelated novelty. However, given that previous studies have not systematically controlled the perceptual relatedness between targets and lures, it remains unclear whether varying the perceptual overlap between the two stimuli would influence the strength of the MTL's novelty signal with respect to false memories.

One critical issue in the aforementioned perceptual false memory studies is that 'relatedness', has typically been defined as membership within a given category of stimuli (e.g., chairs, dogs). Despite overlap in category membership, there likely exists a fair degree of variance amongst related lures with respect to perceptual overlap with the target(s). We posit that this variance may be a critical factor in elucidating the neural components mediating false memories. To that end we aim to clarify and extend previous findings with regards to the neural correlates underlying false