A SYSTEMATIC MEASURE OF SIMILARITY ON FALSE MEMORIES

A Thesis in
Psychology
by
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Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Master of Science

August 2015
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ABSTRACT

The ability to accurately remember previous experiences and differentiate between previously encountered and new information is critical to maintaining an accurate memory for past experiences. However, research has shown that information that shares similarity or relatedness contributes to false memories. Despite the contribution that relatedness or similarity plays in forming false memories, no one has systematically measured or paid close attention to the perceptual relatedness of items in false memory studies. Measuring relatedness of critical lures (i.e., how related is a chair shown at encoding to other non-studied chairs shown at retrieval that produce false alarms) can provide information on item relatedness contributes to the development of false memories. Using a modified perceptual false memory paradigm, the current study aimed to elucidate the cognitive and neural mechanisms underlying both true and false memory retrieval, as well as the influence of perceptual relatedness of lures on false retrieval, in a sample of young adults. Our results converge with previous studies in finding that true and false memories engage many of the same regions, when relatedness is not considered. Furthermore, we replicated previous research showing that there is distinct neural activity supporting true versus false memories. Altogether, similar to previous studies, our study revealed true memories, compared to false memories, to be associated with regions involved in evaluation, accurate reconstruction, and recapitulation of item-specific details of the encoding event. In contrast, gist processing, monitoring, and decision-making regions accompanied false memories, suggestion the strong involvement of gist-based level processing. Unique to our study, we also examined the role of systematic increases in perceptual relatedness/similarity in false memories on neural recruitment supporting false memories. Together, results revealed many perceptual and constructive processes that contribute to false memories, identifying unique regions within the false retrieval network that modulated related false memories, as a function of relatedness.
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ACKNOWLEDGEMENTS

I would like to express tremendous gratitude to my advisor, Dr. Nancy Dennis, for her steadfast support and guidance throughout this project. I would also like to thank the members of my committee, Drs. K. Suzanne Scherf and Reginald Adams, Jr., for their invaluable support. I am extremely thankful for all of your guidance and training throughout this process and thus have made tremendous strides in my writing and critical thinking, as well as my presentation skills. I would also like to acknowledge the National Science Foundation for granting me support during the course of this project (#DGE1255832). Additionally, I would also like to give many thanks to my colleagues in the Cognitive Aging and Neuroimaging Lab, Christina Webb, Caitlin Bowman, and the undergraduate RAs. You have played fundamental roles in your own unique ways to this project, including your involvement in experimental design and data interpretation, as well as providing constructive feedback along the way. Lastly, I would also like to thank my family and friends for their continued support and confidence in me.
Chapter 1

Introduction

The ability to accurately remember previous experiences and differentiate between previously encountered and new information is critical to maintaining an accurate memory for past experiences. For example, when taking medication, it is important to avoid confusing your new medication with old medication that may have similar names or purposes. However, research has shown that information that shares perceptual similarity or relatedness contributes to false memories produced by gist-based processes (i.e., memory for general features of an episodic event). A false memory is when an individual incorrectly claims to have previously encountered a novel object or the individual remembers something as having occurred in the past when in fact it never happened. For example, in famous Ronald Cotton case, Mr. Cotton was misidentified in a line-up and convicted as the man who raped a young woman, Jennifer Thompson. Mr. Cotton was innocent of the crime, but shared similar facial features of the man who actually convicted the crime. The misidentification of Ronald Cotton occurred, in part, because Mr. Cotton shared many similar facial features to the true assailant, Bobby Poole. When Ms. Thompson was presented with Mr. Cotton’s face in a lineup, she recognized it as a familiar face – not because she saw it previously, but because of the shared similar features with Mr. Poole.

All in all, Ms. Thompson had a false memory for Mr. Cotton. Because individuals are likely to remember the general features of one’s face instead of the precise intricate details that make up individual faces, Mr. Cotton was mistaken for Mr. Poole, who was not present in the line-up. Mr. Cotton was released 11 years later due to DNA evidence, an element that is very unique and distinguishable amongst people. Like DNA, we all share unique facial features that differentiate us from others. Nevertheless, people tend to remember the overall image instead of specific features of new faces, which may cause memory errors due to the reconstructive nature of our memories.

The key to false memories is that people believe it actually happened or is
absolutely certain about the person they are identifying. Most often, the false memory is not completely without precedence. In most cases an event highly related or an individual highly similar, but not identical to that which was falsely retrieved, actually did occur.

Despite the contribution that relatedness or similarity plays in forming false memories, no one has systematically measured or paid close attention to the relatedness of items in false memory studies. Understanding the neural mechanisms mediating the effect of relatedness in false memories, combined with research on true memories, can provide valuable insight into fundamental mechanisms of encoding and retrieval processing of this process. The current study sought to elucidate the cognitive and neural processes underlying the systematic increase in relatedness of false memories, with a focus on the role of gist processing as it relates to perceptual memories in young adults.

**Theories and Behavioral Research**

One prominent theory of false memories, the Fuzzy Trace Theory, suggests that both forgetting and false memory errors result as a consequence of the same underlying shift in cognitive processing – an overreliance on familiarity or gist memory (i.e., memory for general features of an episodic event) at the expense of item-specific memory (i.e., memory for specific details of the event). These errors reflect the mechanisms that play an important role in organizing memory as well as related gist-based processes that promote the recollection of thematic information (Deese, 1959; Reyna & Brainerd, 1995; Roediger & Mcdermott, 1995). These findings indicate that memory distortions are based on the means of adaptive cognitive processes that contribute to the efficient and flexible functioning of memory (Addis, Wong, & Schacter, 2007; Schacter, Guerin, & St Jacques, 2011). That is, memory can result in false recollection since individuals recall information predominately based on familiarity, and less on specific perceptual details of the item or of the event. As a result, people will falsely recollect information, even with high confidence (Dennis & Cabeza, 2011).
Behavioral studies show that the processing of relatedness or similarity contribute to false memories when information is thematically related to previously studied information (Koutstaal et al., 2003; Koutstaal & Schacter, 1997; Koutstaal, Schacter, Galluccio, & Stofer, 1999; Robinson & Roediger, 1997; Sugrue & Hayne, 2006). Specifically, Koutstaal and Schacter (1997) examined the recognition performance of older and younger adults for related and unrelated detailed colored pictures of objects based on categorization. The pictures included objects from 20 different object categories, with each category comprising a total of 21 different exemplars. Explicitly, there were 21 pictures of cars, 21 pictures of cats, 21 pictures of children, etc. In addition, there were 30 pictures of unrelated objects (e.g., a painted wine jar and a unicycle). Results showed that participants falsely recognized lures from studied categories, compared to unstudied categories. As a result, this study showed that reinforcing the gist or category level representations by encountering multiple exemplars of a category of objects could lead to false recognition of items that are thematically related to the studied exemplars.

Robinson and Roediger (1997) also examined the effect of manipulating the number of associated words presented on false recall and false recognition. In this study, the researchers manipulated list length of associated lists and number of associated words within the list in two experiments. In detail, experiment 1 manipulated the number of associated words in a study list. Lists consisted of 3, 6, 9, 12, and 15 words and participants were asked to recall each list after a 30 second delay, then an overall recognition task including studied and critical items followed the presentation and recall of all the lists. Experiment 1 showed that the probability of false recall increased with increasing list length. Experiment 2 held list length constant while varying the number of associated words studied increased, unaffected by the presence of the filler/unrelated words. Results from experiment 1 were replicated and the rate of intrusions in recall increased gradually as the number of associated words studied increased, unaffected by the presence of the filler/unrelated words. Together, results showed increased false memories as similarities between exemplars increased.
Similarly, Sugrue and Haynes (2006) explored the performance of participants across varied lengths of studied lists using the Deese-Roediger-McDermott (DRM) paradigm. For example, participants studied eight DRM lists comprised of either seven words (short list) or fourteen words (long list). Compared to the short list, participants showed a higher rate of false recognition than in the long list. Generally, this study showed that the amount of related information and the percentage of items falsely recognized increase the number of memory errors.

Another relatedness paradigm used to examine false memories is the perceptual relatedness false memory paradigm. This paradigm induces a perceptual gist (e.g., the overall shape) of items to examine false memories associated with recognition responses to critical lures. Essentially, these critical lures share similarities (i.e., perceptual overlap) or common features to items that were presented during encoding. Behavioral studies show that as items become more and more similar, false memories increase.

**Previous Neuroimaging Research**

Research has found much commonality in neural activity mediating true and false memories for related items. One of the most universal findings generated from false memory studies is the extensive overlap in the neural networks that mediate both true and false memories (for review, see Dennis et al., 2015). Overall researchers find widespread overlap in neural activity mediating both memory processes, including bilateral frontal and parietal regions, occipital cortex, lateral temporal cortex, bilateral caudate and hippocampus/parahippocampal gyrus (PHG). This extensive overlap in regions may suggest that false memories engage many of the same processes as true memories (i.e., semantic and visual processes). This widespread overlap in neural activity mediating both true and false memories has been attributed to several factors, including the fact that targets and related lures share similar properties (i.e., shared semantic meaning and/or perceptual similarity) (e.g., Garoff-Eaton, Slotnick, & Schacter, 2006), the engagement of highly similar retrieval-related evaluation and monitoring processes (e.g., Atkins & Reuter-Lorenz, 2011), retrieval of contextual
information (e.g., Okado & Stark, 2003), and evidence that both types of memories are supported by above threshold familiarity processing (e.g., Kahn, Davachi, & Wagner, 2004). Due to the similarity between targets and related lures, stimuli in these relatedness paradigms are therefore likely to evoke comparable retrieval-related activity within brain regions mediating both perceptual and semantic processing.

Furthermore, common activity in frontal regions has been associated with retrieval effort and monitoring processes, presumed to operate independently of retrieval success (e.g., Atkins & Reuter-Lorenz, 2011). Therefore, it is not surprising that such activity would underlie both true and false memory retrieval, as these processes support decision making, not necessarily the accuracy of a given decision or memory. Similarly, common activity in the precuneus and lateral parietal cortex are interpreted as reflecting general “recovery operations” (Cabeza, Rao, Wagner, Mayer, & Schacter, 2001) or the general feeling of oldness (Atkins & Reuter-Lorenz, 2011) that also occurs independent of retrieval accuracy. Overall, studies that show common activity between true and false memories emphasize that activity across several brain regions can reflect language, perceptual, and monitoring processes that are independent of the encoding history of the stimuli. Examining false memories throughout the lifespan is imperative to memory research considering this overlap in behavioral characteristics shared among both true and false memories and their high rate of occurrence in memory tests (McCabe, Roediger, McDaniel, & Balota, 2009).

Despite the aforementioned overlap in neural correlates of true and false memories, many studies also find differences in neural regions that mediate true and false memories, independently. One of the most notable differences is increased activity in sensory cortices associated with true but not false memories (Abe et al., 2008; Atkins & Reuter-Lorenz, 2011; Cabeza et al., 2001; Dennis, Bowman, & Vandekar, 2012; Moritz, Glascher, Sommer, Buchel, & Braus, 2006; Schacter, Reiman, et al., 1996; Slotnick & Schacter, 2004). Greater activation of sensory processing regions for true compared to false retrieval has been interpreted in accord with the ‘sensory reactivation hypothesis.’ This hypothesis, founded in behavioral research, argues that true memories are
associated with more sensory and perceptual details, compared to false memories (e.g., Marche, Brainerd, & Reyna, 2010; Mather, Henkel, & Johnson, 1997; Norman & Schacter, 1997).

This hypothesis suggests that, by virtue of having been presented previously, true memories will elicit reactivation of the encoding episode in sensory regions that were involved in their initial encoding. This finding has been observed across several traditional memory studies (e.g., Vaidya, Zhao, Desmond, & Gabrieli, 2002; Wheeler, Petersen, & Buckner, 2000). Hence, because false memories are not previously presented, it is expected that they will not be accompanied by this heightened sensory signal. For example, Schacter and colleagues (1996) utilized an auditory verbal encoding task of related words. Greater activity for true memories was found in the temporal-parietal junction, a region associated with auditory processing. This finding was interpreted as reflecting participants’ retrieval of the auditory or phonological aspects of the item’s presentation during the study phase. Several ERP studies have also observed differential activity over posterior cortices for true and false memories, supporting greater amounts of sensory processing for true compared to false memories (Curran, Schacter, Johnson, & Spinks, 2001; Fabiani, Stadler, & Wessels, 2000; Nessler & Mecklinger, 2003; Nessler, Mecklinger, & Penney, 2001; Walla, Endl, Lindinger, Deecke, & Lang, 2000).

Recent studies have shown dissociation in the recruitment of early vs. late visual processing regions for true vs. false memories. Particularly, activity in early visual processing regions (BA 17 and 18) is greater for true compared to false memories, [while, as noted above, activity in late visual cortex (i.e., BA 19 and 37) is commonly active for true and false memories] (Dennis et al., 2012; Slotnick & Schacter, 2004). While both early and late visual cortex are associated with object perception and identification, early visual cortex has been associated with recapitulation of a sensory signature (Buckner & Wheeler, 2001; Rugg & Wilding, 2000; Vaidya et al., 2002) while late visual cortex has been linked to retrieval of general object identity and meaning (Vaidya et al., 2002; Wheeler & Buckner, 2003; Wheeler et al., 2000). Consequently, in
reference to true and false memories, common activity has been interpreted as reflecting retrieval of common perceptual details and conscious processing of an item as 'old', whereas activity in early visual cortex has been interpreted as reflecting retrieval of perceptual and sensory details associated with the encoding episode (Dennis et al., 2012; Slotnick & Schacter, 2004; Stark, Okado, & Loftus, 2010).

Perceptual processing in late visual cortices (BA 19, & 37) has also been suggested to reflect processing that contributes to the conscious experience of memory, which is independent of true “oldness” (Slotnick & Schacter, 2004). Others also suggest that such processing is likely to reflect successful retrieval of the general properties of originally studied items such as shape and color (Garoff-Eaton et al., 2006) or those involving the semantic label or general category (e.g., fruit, bird) to which the item belongs. As such, common activity in semantic processing regions, such as left temporal gyrus and dorsolateral PFC, has often been interpreted as retrieval of these semantic labels (Dennis, Kim, & Cabeza, 2008b; Garoff-Eaton, Kensinger, & Schacter, 2007; Kim & Cabeza, 2007c; von Zerssen, Mecklinger, Opitz, & von Cramon, 2001).

Additionally, Slotnick and Schacter (2004) used computer generated abstract shapes to examine the association of greater sensory/perceptual details associated with true compared to false memories. This study found widespread overlap in the sensory and reconstructive processes that support true and false recognition. Both true and false recognition were associated with activity in late visual processing regions (BA 37), where these regions potentially supported “old” responses, independent of accuracy. This common overlap was also evident in PFC, parietal cortex, and hippocampus.

Likewise, Gutches and Schacter (2012) used categorized pictures to investigate the neural correlates of false recognition based on the degree of related information. This study focused on false recognition of related items. The authors found that, as the relatedness amongst items was strengthened at encoding, the false alarm rate increased, as did activation in both the hippocampus and visual processing regions (BA 17 and 37). Interestingly, high levels of relatedness had the opposite effect for true memories. Increasing relatedness amongst items led to reduced visual activity, which
the authors interpret as reflecting evidence that true memories rely on analyzing individual perceptual features and that this may be best supported under low relatedness conditions. Overall, for true memories, regions in the middle occipital, middle temporal, and posterior parietal cortex linearly modulated participants’ activity according to the number of related encoded items. False memories also elicited greater modulation in activity as a function of the encoded set size in visual, parietal, and hippocampal regions.

Though previous studies find common activity in MTL regions, several studies also find that the MTL supports retrieval only of true memories (Cabeza et al., 2001; Dennis et al., 2012; Dennis et al., 2008b; Giovanello, Kensinger, Wong, & Schacter, 2009; Kahn et al., 2004; Kensinger & Schacter, 2006; Kim & Cabeza, 2007c; Paz-Alonso, Ghetti, Donohue, Goodman, & Bunge, 2008). Dennis and colleagues (2012) for example, examined the role of the MTL in both true and phantom recollection through color pictures of common objects. During study, 8 exemplars from a given category of items (e.g., dogs) were presented to participants. At test, participants were presented with a subset of studied exemplars and new exemplars and were asked to determine which items were previously presented. Using functional connectivity analyses, this study found common anterior hippocampus/PHG activity for both true and false memories and greater right hippocampal and early visual cortex activity for true, compared to false recollection. The authors suggested that increased hippocampal activity represented more details retrieved for true memories or the accurate reconstruction of details that support true recollection. These results suggest that even though the MTL mediates retrieval processes leading to both true and false recollection, the hippocampus proper and early visual cortex were able to distinguish between detailed recollection of true and false memory.

While many studies find no differential activity in MTL for true and false memories, as mentioned, those that do, find increased MTL for true more so than false memories (Cabeza et al., 2001; Dennis et al., 2012; Dennis et al., 2008b; Giovanello, Kensinger, et al., 2009; Kahn et al., 2004; Kensinger & Schacter, 2006; Kim & Cabeza,
Some studies suggest that greater MTL activation for true memories reflects greater recovery of sensory details associated with true memories (Cabeza et al., 2001; Kahn et al., 2004; Okado & Stark, 2003), while others suggested this neural increase reflects the role of the hippocampus in binding together true details from past events (Kensinger & Schacter, 2006), or recollection processes (Dennis et al., 2012; Kim & Cabeza, 2007c).

Taken together, because some studies find no MTL differences for true and false memories (Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997; Slotnick & Schacter, 2004; Stark et al., 2010), there is no clear or adequate theory explaining the role of the MTL in false memories. Overall, research has shown that the MTL tracks relatedness. However, only some studies show differences in MTL activity for true compared to false memories, while others do not show any difference. The reason for this may be due to the lack of systematic differences in the types of lures being used in these studies. As a result, because of the systematic pattern of overlap in the related lures in our study, we will be able to examine this issue more directly.

Similar to early visual cortices being involved with only true memories, the only region that has consistently shown greater activity for false compared to true recollection is the PFC (Cabeza et al., 2001; Garoff-Eaton et al., 2007; Kensinger & Schacter, 2006; Kim & Cabeza, 2007c; Kubota et al., 2006; Okado & Stark, 2003; Schacter, Buckner, et al., 1997; Schacter, Reiman, et al., 1996; Slotnick & Schacter, 2004). Depending on the location of the activity within the PFC, studies attribute increase PFC activation to monitoring, reconstructive processes, and semantic elaboration. For example, Garoff-Eaton and colleagues (2007) found increased activity in left inferior, middle, and medial frontal gyrus for false memory associated with lures that were conceptually related to encoded items (e.g., silver, bronze), but not when the lure was perceptually related to encoded items (e.g., bell, tell). Since both types of false memories should require equivalent monitoring and evaluation, researchers attributed the increased left PFC activity to the retrieval of conceptual information that pertained
to the items’ meaning and relatedness, which accompanies both the studied items and the related lures.

Several neuroimaging studies support the idea that false memories are mediated by either familiarity or the relatedness between items that is associated with the encoding theme (Dennis et al., 2008b; Duarte, Graham, & Henson, 2010; Garoff-Eaton et al., 2007; Kim & Cabeza, 2007a, 2007c; Moritz et al., 2006). False memory activity in regions outside of the prefrontal cortex has also been associated with processing relatedness. For example, Kim and Cabeza (2007b) used a modified version of the DRM false memory paradigm to examine the influence of confidence on true and false memories. The researchers found that fronto-parietal activity mediated high confidence false memories and concluded that false memories are induced from a strong feeling of familiarity that is associated with critical lures as they share similarities with items from encoding. Generally, results suggest that when critical lures are semantically or perceptually related to studied items, this similarity or relatedness induces a sense of familiarity that is strong enough to form the basis of a false memory.

Consistent with prior studies of false memory of related information, we anticipate that relatedness-based errors will arise due to the engagement of perceptual and constructive processes. Our approach based on systematically manipulating relatedness should be especially useful for interpreting the current mixed results in the literature. Specifically, mixed results with some studies demonstrating that the MTL and other regions are engaged by both accurate and false memories (e.g., Addis et al., 2007; Garoff-Eaton et al., 2006; Schacter, Buckner, et al., 1997) while some suggest that the regions are engaged more by true than false memories (e.g., Cabeza et al., 2001; Giovanello, Schnyer, & Verfaellie, 2009; Kensinger & Schacter, 2005; Schacter, Savage, Alpert, Rauch, & Albert, 1996). It is possible that the MTL and/or visual regions respond to the gradation of relatedness among similar items, such that these regions may show a parametric increase as the items’ relatedness increases.

While previous studies have begun to identify shared neural substrates for true and false memory for related information, relatedness has been treated in an all-or-
none fashion and without varying the differences of relatedness between items. For example Koutstaal and colleagues (1997) and Dennis and colleagues (2012) observed false memories for related and unrelated items, however, they did not determine whether said items within a category were different from each other based on relatedness. Similarly, Gutchess and Schacter (2012) investigated false recognition as a function of relatedness/gist strength by varying number of items in a category. Even Slotnick and Schacter (2004) used computer generated abstract shapes to observe difference in visual cortical activity between true and false recognition. Still yet, none of these studies controlled for relatedness between items (targets and related lures).

Overall, previously administered paradigms have not been able to measure the systematic change of the relatedness of related lures and very few have examined the neural correlates of such process. Different levels of relatedness may contribute distinctively to false memories, which can assist with identifying differences in neural correlates for false, compared to true memories. Furthermore, though several neural regions are engaged when there is some degree of overlap between true and false memories, there may only be a subset of regions that are increasingly engaged as relatedness is strengthened. It is pertinent to examine these regions’ role in order to better understand the claim that memory distortions often reflect adaptive cognitive processes, as well as understanding the role of relatedness in these induced false memories.

The aforementioned limitation to previous studies developed largely because of methodological limitations such as insufficient number of false alarms and the lack of a systematic measure of similarity between false alarms. The current study overcame this restriction by using a parametric modulation approach and systematically manipulated the degree of similarity/relatedness between targets and related lures. Precisely, we used a modified version of perceptual false memory paradigm by using morphed faces to systematically control perceptual relatedness across related lures (see figure 1). Using this parametric modulation approach, we identified regions that responded to the degree of relatedness of the related lures, which allowed us to selectively identify the
cognitive processes and neural substrates associated with increased levels of relatedness

Similar to the DRM paradigms, memory distortion for faces has been investigated using items constructed by combining the facial features of separately studied faces; thus, it was composed of previously memorized components. False alarm rates for these combined-face stimuli were typically higher than those for completely new faces, but lower than the hit rates of studied faces. This suggests that memory errors for the combined faces are mainly based on familiarity processes in the absence of the precise recollection process of episodic memory (Clark & Gronlund, 1996). Using a similar modified version of the DRM paradigm (categorized pictures paradigm), Koutstaal and Schacter (1997) investigated false memories for pictures. The researchers reported higher levels of false recognition for related lures.

**Face Memory**

While the main impetus for the current study was to investigate the effects of relatedness on false memory processing, the current design anticipated testing this within the context of face memory. This stimulus set brings up additional considerations when formulating neural predictions. In our society, face recognition is a fundamental and vital skill for communicating. Throughout the lifespan, face recognition plays a significant role in everyday situations as the proportions and expressions of the human face are important to identify origin, emotional tendencies, health qualities, and some social information and interaction. For example, it is critical to remember co-workers, individuals met at events, or a criminal in a crime to which one witnesses. In all cases, it is extremely important to accurately recall the exact individual and not merely someone with similar height, stature, or facial features.

**Face Perception/Processing**

Strategies of face processing is divided into two main subtypes: configural and featural (Maurer, Grand, & Mondloch, 2002). Configurational processing signifies
perceptions of the spatial relations among the internal features while featural or item-specific processing, refers to perceptions of the shapes of individual features. Human faces share basic individual features including eyes, nose, and mouth, as well as consistencies in the arrangement of these features (i.e., eyes above the nose and mouth below the nose). Nevertheless, the shapes of these features and the spatial distances between them differ among individuals. According to Diamond and Carey (1986), the spatial distance among facial parts is critical for accurate identification and differentiation among faces. Thus, to correctly identify a particular person's face, information about both the specific facial features and the specific configuration among features must be encoded. Evidence suggests that both featural and configurational data are essential to the processing, as well as the accurate and proficient recognition of upright faces. However, if both featural and configurational processing interact during face recognition, it can be presumed that the two types of information may be processed in separate brain regions, but connected through neural networks that function in a collaborative way.

Though most adults are able to recognize and discriminate between faces at a glance, due to reconstructive memory processes, like most information stored in memory, face recognition is highly susceptible to false memories. For example, in line with the Fuzzy Trace theory, one may remember the general details of the individual who committed the crime instead of specific unique details of that individual. Research shows that people have significantly poorer memory; encoding and recognizing new or unfamiliar faces (the types of faces typically witnessed during a crime) (Hancock, Bruce, & Burton, 2000). Consequently, one may develop only a gist (i.e., general features) memory trace of a person or event, which may lead to false identification of another individual.

Understanding the neural foundation of face false memory is vital in understanding the role of faces in false memory, especially when face shares common features. Neuroimaging studies show that the occipito-temporal regions are particularly important for face processing (Haxby, Hoffman, & Gobbini, 2000; Kanwisher,
McDermott, & Chun, 1997; McCarthy, Puce, Belger, & Allison, 1999), along with other contributing areas (Leonard et al., 1985; Rajah et al., 1999; Seeck et al., 2001; Ishai et al., 2002; Iidaka et al., 2012). Additionally, bilateral anterior regions show sensitivity to identity change. For example, Rotshtein and colleagues (2005) observed less activity in inferior occipital gyrus (IOG) and right occipital face area (OFA) when the physical properties of a face were identical. The authors interpreted this to be suggestive that bilateral IOG and right OFA are primarily sensitive to physical attributes of faces and play an important role during the structural encoding of faces. On the other hand, in relation to face identity, IOG, right OFA, and FFG showed sensitivity to identity change, even when physical changes were equally big holding structural change constant. This suggests that FFG, in addition to OFA and IOG, may play a significant role in encoding the identity of a face, across huge variations in visuoperceptual information, differentiating between individual faces. Given the role of these regions, we hypothesized their involvement during true retrieval of faces.

Regarding false memories, Iidaka and colleagues (2012) examined related and unrelated false memories for faces and found that regions including left superior parietal and left inferior frontal gyrus were active for related false recognition. Particularly, the anterior cingulate cortex (ACC) was engaged in the false recognition of related items that have a perceptual resemblance to the old items, causing a response conflict between the items. Additionally, the neural correlates of false memories for faces partly overlapped with those for true memories in terms of localization of the brain structures, including the left amygdala and the bilateral orbital cortices. In contrast, activity in a specific region of the ACC may represent, according to the authors, some aspects of response conflict and mnemonic processing of falsely recognized memory items. This was concluded since participants’ activity levels were significantly related with their performance speed. Nevertheless, without any direct contrasts or conjunction analyses, it is uncertain the extent to which this activity is unique to related false memory or is part of a network that reflects more general processes involved in false memories.
**The Present Study**

Reconstruction processes that lead to false memories may be a result of the similarity between items and still no studies have examined how similarity amongst items induces false memories. The current study aims to investigate a systematic measure of change in similarity associated with false alarm rates. The approach in this study involved manipulating perceptual relatedness will be extremely helpful in providing evidence on the mixed results mentioned above in the literature. We will use event-related functional magnetic resonance imaging to compare the neural activity associated with both true and false memory processes. Above all, this study will examine systematic increases in perceptual relatedness; fMRI analyses will take advantage of the parametric approach to examine systematic increases in relatedness.

Behaviorally, we predict that differing levels of relatedness will reveal that participants exemplified a greater pattern of false alarms as a linear function of increased relatedness. Neurolly, we expect to replicate previous common activity for both true and false memories, along with differential findings. Precisely, differences in activity underlying true more than false recognition, collapsed across relatedness, should recruit early visual cortex, occipito-temporal regions and parahippocampal because increased engagement of sensory cortices should be associated with true compared to false retrieval. Areas demonstrating featural face processing such as the occipito-temporal regions, posterior superior temporal sulci and anterior temporal regions are expected to show greater activity for true memories. On the other hand, false more so than true recognition, should recruit regions of the frontal cortex, including anterior cingulate and right dorsal and ventral regions of the middle frontal gyri, superior and middle temporal gyrus, indicating general gist processing. The posterior Fusiform should also show greater activity for false memories as this region is implicated with less differentiation in face recognition and inferior occipital regions (holistic face recognition/processing of general features).

Most importantly, we expect parametric increases, as relatedness increase in in frontal, visual, and lateral temporal regions. Specifically, activity in the DLPFC is
expected as this region is implicated in decision-making. The ability to distinguish between an 70:30 morph, for example, may require greater demand than say deciding on a 30:70 morph. Activity in visual regions including fusiform may reflect the role of visual regions in perceiving and recollecting prototypical features. Lateral temporal regions, specifically the hippocampus should exemplify this graded response as it has been shown to underlie the processing of perceptual features. Regions of the extended Face processing network, including the vmPFC and Posterior Cingulate Cortex for overall familiarity and episodic memories.

Chapter 2

Methods

Participants

Twenty-five right-handed young adults were recruited from The Pennsylvania State University community and received financial compensation for their participation. All participants were screened for history of neurological disorders and psychiatric illness, alcoholism, drug abuse, and learning disabilities. The current analysis included all 25, right-handed participants (17 females) between the ages of 18-31 years old [mean age = 23 years, (SD=3.74)]. All participants provided written informed consent and all procedures were approved by the Pennsylvania State University Institutional Review Board.

Stimuli

<table>
<thead>
<tr>
<th>% of parent faces</th>
<th>100:0</th>
<th>70:30</th>
<th>50:50</th>
<th>30:70</th>
<th>0:100</th>
<th>0:0</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stimuli Type</td>
<td>Parent X</td>
<td>Morph</td>
<td>Morph</td>
<td>Morph</td>
<td>Parent Y</td>
<td>New</td>
</tr>
<tr>
<td>Trial Type</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>--</td>
<td>1</td>
</tr>
</tbody>
</table>
The stimuli consisted of 228 pictures of adult (ages 18 - 39), equal numbers of male and female faces with neutral expressions. The faces were chosen from The Color Facial Recognition Technology (FERET) database (Phillips, Wechsler, Huang, & Rauss, 1998) and the AR Face database (Martinez & Benavente, 1998). The faces were morphed together using Abrosoft Fantamorph. The background of each image was removed and pictures were cropped and resized to an approximate size of 384 x 514 pixels. Images were presented focally and equated for resolution. In order to control for similarity among morphed faces, morphing took place between two faces of the same gender and race. Half of the faces were Caucasian and the other half were a mixture of minority races (African Americans, Indians, Asians, and Hispanics). All faces were morphed within race and gender.

Out of the 204 faces, 192 faces were used to create the stimuli for the study portion of the experiment and the other 12 were only used during the retrieval portion of the study as unrelated lures. 96 of the original 192 faces were used as parent faces (parent X faces); original faces that were combined at varying percentages with the other 96 parent faces (parent Y faces) to create 288 related morphed faces in total (3 morphed faces per parent pair). Only one of the 3 morphed faces were used at retrieval per parent X and parent Y combo. See figure 2 for stimuli creation details.¹

During encoding participants viewed 96 original unmorphed (parent X) faces. The parent faces were the original, unaltered faces used for the morphing procedure and were presented as target faces during retrieval. All faces were morphed within the same racial grouping and the faces were blended at percentages of (70:30), (50:50), and (30:70) with the first number in each set representing the percentage of one parent face in a morphed face and the second number in each set representing the percentage of the second parent face in the morphed face. Twelve of each morph blend (across race and sex), for a total of 48 were used during retrieval as related lures, while 48 faces from each set (Parent X) were used as targets during retrieval.

¹Figure 1 shows an example of the varied levels of related lures for each face. However, through piloting, this example’s 70:30 related lure might not have been perceptually discriminable from its target face. As a result, this 70:30 face was not used; instead, this example’s 50:50 or 30:70 related lure was used.
Furthermore, in order to ensure that each related lure was reliably discriminable from its target counterpart, we piloted as well as had each participant complete a perceptual discrimination task. In this task, an independent set of participants viewed each target and related lure pair and decided whether they were identical or different. According to our behavioral and pilot data, participants were able to successfully distinguish between the targets and their 70:30, 50:50, or 30:70 counterpart. This discrimination data demonstrated that participants could actually perceive the physical difference between the morphs and target faces. Hence, we are assured that, for example, the 70:30 related lures were not perceived as the same or identical to their target face counterparts.

A dynamic face localizer task (Hasson, Nir, Levy, Fuhrmann, & Malach, 2004) was used to map face-sensitive regions in each participant. It was a silent, fluid blocks of short (15-s) movie vignettes (32 in total). These blocks of vignettes contained scenes of either four experimental conditions, including people and faces (video clips of individuals laughing, angry, neutral, etc.) buildings (video clips of various buildings
including skyscrapers, houses in residential and business areas etc.), navigation through open fields (video clips of planes of meadows, mountains, ocean etc.), and miscellaneous common objects (video clips of watches on an individual hand, moving cars, running faucets etc. The block design was utilized for stronger signals with better statistical power. Overall, this task allowed for a more natural exploration of the visual environment, compared to the static photographs often used in previous neuroimaging studies. This task also provides robust category-selective activation in ventral temporal regions (Avidan, Hasson, Malach, & Behrmann, 2005), which is of great importance in our study.

**Procedure**

Encoding, retrieval and the dynamic face localizer took place in the scanner. Images were projected onto a screen that participants viewed through a mirror attached to the head coil. All images were presented in the center of the screen with rating scales (i.e., 1 – 4, where 1 corresponds to highly unusual and 4 is highly typical) displayed below each image. Behavioral responses were recorded using a 4-bottom response box. Images were displayed by COGENT in MATLAB (Mathworks). Scanner noise was reduced with headphones and earplugs, and cushioning was used in the head coil to minimize head motion.

During encoding participants were asked to rate each face based on how typical (difficult to spot in a crowd) or atypical (distinct or easy to spot in a crowd) the face appears. Encoding images was presented for 4 seconds and the participant made the typical or atypical rating of the faces during that time, while the face is still on the screen followed by a variable interstimulus interval. The duration of encoding approximated about 15 minutes, across 4 runs. Following encoding, there was a 20-minute delay/interference period during which structural images (MPRAGE & DTI) were acquired and the instructions of the retrieval task were reiterated.

Subsequently, during retrieval, participants were shown 112 faces including 48 targets, 12 70:30 related lures, 12 50:50 related lures, 12 30:70 related lures and 12 0:0
unrelated lures (novel faces). Each face was displayed for 4 seconds while participants made recognition memory responses using old/new and confidence ratings as mentioned above. Participants responded “old” with high or low confidence if they could recollect specific details about the faces or their thoughts or feelings during the initial presentations. Participants responded “new” with high or low confidence if they believed the face was not shown during the study session. The images were pseudorandomly sorted to ensure that no more than 3 images from any one trial type appeared in a row with varied inter-trial interval between 1 to 8 seconds.

Lastly, the dynamic face localizer occurred immediately after retrieval. Again, it was a silent, fluid blocks of short (15-s) movie vignettes (32 in total). These blocks of vignettes contained scenes of either four experimental conditions, including people and faces, buildings, navigation through open fields, and miscellaneous common objects. The duration of the localizer was approximately 9 minutes. No responses were required; participants were instructed to simply pay attention to each of the short vignettes.

**Image Acquisition**

Images were acquired using a Siemens Prisma Fit 3T scanner equipped with a 12-channel head coil. Functional EPI images were then prescribed parallel to the AC-PC plane with a 30-degree steep angle. This allowed for a better signal-to-noise ratio in temporal cortex. Echo-planar functional images for encoding and retrieval were acquired using a descending acquisition, 2500ms TR, 25ms TE, 240mm FOV, a 80^2 matrix, 42 axial slices with 3mm slice thickness resulting in a 3mm isotropic voxels. For the functional movie localizer paradigm, Echo-planar functional images were acquired using a descending acquisition, 3000ms TR, 30ms TE, 240mm FOV, a 80^2 matrix, 42 axial slices with 3mm slice thickness resulting in a 3mm isotropic voxels. An MPRAGE was acquired with a 1650ms TR, 2.03ms TE, 256mm field of view (FOV), 256^2 matrix, 160 axial slices, and 1mm thickness for each participant.

**fMRI Analysis**

Functional data were preprocessed and analyzed with SPM8 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm). Images were first checked for scanner and movement artifacts using a time-series diagnostic function TSDiffAna (Freiburg Brain Imaging) in MATLAB (Mathworks). Time-series data were realigned and images were then coregistered to the individual’s T1 image before being spatially normalized to a standard stereotaxic space using the Montreal Neurological Institute (MNI) EPI template implemented in SPM8. Finally, the volumes were spatially smoothed using an 8-mm isotropic Gaussian kernel.

Trial-related activity was modeled with a general linear model (GLM) using a stick function corresponding to trial onsets convolved with a canonical hemodynamic response function (hrf). Random effects analyses allowed for the assessment of distinct and common patterns of activation. Parametric analysis was conducted at the fixed effect level (using degree of relatedness) as a covariate of interest, to test the linear trends across relatedness for false alarms. Individual regressors were collapsed across confidence levels (‘Old-High,’ ‘Old-Low,’ ‘New-Low,’ and ‘New-High’) for false alarms and misses only, resulting in six regressors (Hits-2, Misses, False Alarms, and Correct Rejections-2. No response trials and motion parameters were modeled as regressors of no interest. The mean number of trials in each regressor of interest was Hi-Hits (23), Lo-Hits (13), Misses (12), False Alarms (19), Hi-Correct Rejections (23), and Lo-Correct Rejections (21).

The neural activity associated with each contrast of interest was directly assessed at an individual voxel threshold of p < .005 in combination with a cluster extent threshold of 10 voxels (Lieberman and Cunningham, 2009). We utilized both the traditional contrast approach and a parametric modulation approach in our fMRI analysis in order to systematically assess the neural correlates mediating false memories as a function of relatedness in a given set of regions of interest (mentioned above). As a first step we assessed the neural correlates mediating true and false retrieval (collapsed across both levels of confidence and degrees of relatedness). As
such constructed a model that models Hits, False Memories, Correct Rejections and Misses. This model allowed us to look at the neural activity associated with each trial type compared to baseline. A comparison between Hits and False Alarms allowed us to investigate unique neural activity associated with each type of memory response within various brain regions. Finally, a conjunction analysis was created with Hits and False Alarms in order to assess overlap between the two memory responses.

Parametric modulation is a special case of the GLM approach of using "user specified regressors" in SPM. Regressors are used to study session specific adaptation in brain activity, general effects of time on brain activity and brain-behavior correlations effectively. The parametric model will build upon the previous model, modulating the False Alarm regressor with respect to relatedness. In detail, we modeled a linear increase in false alarms as a function of relatedness (0:100 = 1; 30:70 =2, 50:50 = 3, 70:30 = 4). This regressor allowed for the identification of regions whose activity correlated positively (i.e., increasing as relatedness increased) modulating across the different levels of relatedness for false alarms.

Face Localizer Task and ROI analyses

To more closely examine the response pattern of activity within the MTL and the visual cortex (FFA), we conducted ROI analyses within these regions. First, the face-selective ROIs were defined by the weighted contrast [3 × (faces) − (objects + buildings + navigation)], as done in previous studies using this task. In each participant, each contrast was computed on the z-transformed raw signal and was corrected for multiple comparisons using the false discovery rate procedure (Genovese et al. 2002) with q < 0.10. Each ROI was defined independently in each hemisphere in each individual. The face-related ROIs included the set of contiguous face-selective voxels throughout the FG, as determined by the aal atlas. In order to determine the magnitude of category selectivity within each ROI in each hemisphere, separate ROI-based GLMs were conducted for each participant who exhibited identifiable category-selective activation in each ROI. This generated beta weights for each condition (i.e., faces, places, buildings, navigation) for each participant. Face selectivity in the FFA was computed by
submitting these beta weights to the above-mentioned contrast. In our analyses however, we used the group-level masked ROI.

We then used the functionally defined masked from our face localizer of bilateral FFA and an anatomically defined mask (aal atlas in SPM) of bilateral MTL (PHG, hippocampus, and amygdala). For the FFA analyses, we proceeded by using our face localizer task (described above) to examine more closely, the involvement of the face-processing region (FFA) in the visual cortex. In detail, after obtaining a group-level FFA activity from our face localizer task (corrected at FDR .1 – reduced threshold), we used this activity as an ROI within the false alarm parametric contrast, also at a reduced threshold (p<.05 uncorrected). This allowed us to more closely observe the fine-grained involvement of the visual cortex (FFA) in false memories, as relatedness increase. We also performed this analysis within the anatomically defined bilateral MTL ROI.

Additionally, to further investigate how the FFA and MTL responded to true and false memories, we created an additional model consisting of hits, misses, each level of false alarms (2-4; 4 being greatest level of relatedness in related lures), and correct rejections (2-4) as regressors of interest. This model allowed us to explore, in greater detail, the pattern of activity within these regions, for each false alarm regressor, as relatedness increase. We obtained the mean activity within the functionally defined FFA ROI and the anatomically defined MTL ROI, within each contrast (False Alarms) of interest.

Chapter 3

Results

Behavioral

Behavioral responses to targets, related lures, and unrelated lures, as well as the average number of trial types per condition are presented in Table 1. A repeated measures ANOVA of related lures, across the differing levels of relatedness revealed a main effect of condition, showing that participants exemplified a greater pattern of false
alarms as a linear function of increased relatedness \[ F(1, 24)=112.20 \, p<0.001 \]. Post-Hoc pairwise Bonferroni corrected comparisons showed that false alarm rates for the 70:30 related lure significantly differed from all the other lures, 50:50 significantly differed from 70:30 and 0:0 lures, 30:70 significantly differed from 70:30 and 0:0 lures and 0:0 significantly differed from all levels of related lures.

Using reaction time as the dependent variable, a repeated measures ANOVA revealed no significant linear effect of reaction time on correct rejections between the differing levels of related lures \[ F(1,16) = 1.63, \, p = .214 \]. However, we did observe a significant linear reaction time effect with false alarms for the related lures \[ F(1,16) = 4.99, \, p = .040 \]; as relatedness increased, reaction time increased. Participants’ overall false alarm rate to the unrelated lures was significantly lower than that exhibited to the related lures \[ t(16) = 18.84, \, p < 0.001 \], indicating that the high rate of false alarms to related lures was associated with the similarity of the stimuli with respect to the targets and not simply a general tendency for participants to false alarm to all new items.
Imaging

Planned Results

Common activity for True and False Memories

We first assessed the overlap of activations for hits and false alarms compared to baseline in order to assess whether the overlap reported in previous studies for true and false recognition was similar in the current study. Table 2 reports results associated with both true and false retrieval, as well as activity common to both types of retrieval processes. Particularly, when collapsing across relatedness in false alarms, a conjunction analysis of true and false retrieval exhibited common neural activity in the typical retrieval network including bilateral parietal, insula, bilateral inferior and medial frontal gyrus, and occipital regions.

True Greater than False Retrieval

Next, we tested for differences in the activity that exhibited difference between true and false recognition. Results showed that true memories, compared false memories, elicited greater activity in early visual cortex, occipito-temporal cortex and right parahippocampal gyrus. We also examined true greater than false activity only using high confidence hits in order to balance power with the false alarm contrast as well as examine the neural mechanisms normally associated with true recollection. The activity

<table>
<thead>
<tr>
<th>Table 1. Behavioral results</th>
</tr>
</thead>
<tbody>
<tr>
<td>100:0</td>
</tr>
<tr>
<td>-</td>
</tr>
<tr>
<td><strong>Accuracy</strong></td>
</tr>
<tr>
<td>Old-High</td>
</tr>
<tr>
<td>Old-Low</td>
</tr>
<tr>
<td>Combined Old</td>
</tr>
<tr>
<td>New-High</td>
</tr>
<tr>
<td>New-Low</td>
</tr>
<tr>
<td>Combined New</td>
</tr>
</tbody>
</table>

The table reports mean response rates (and standard deviation) to targets (100:0), related lures (70:30, 50:50, 30:70) and unrelated lures (0:0), as well as the average number of trial types per condition. TT = Trial Types
pattern of high confidence hits greater than false alarms remained similar to when collapsing across confidence, but with greater magnitude in some regions’ activity as well as additional clusters of activity in the frontal cortex. Specifically, high confidence hits exhibited greater activity in bilateral hippocampus/amygdala and visual regions, extending into the fusiform gyri (mainly left lateralized), as well as ventro-medial PFC (vmPFC), and left inferior frontal gyri (see table 2).

<table>
<thead>
<tr>
<th>Table 2. True and false retrieval</th>
<th>BA</th>
<th>H</th>
<th>Coordinates (T&amp;T)</th>
<th>t</th>
<th>mm³</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>Y</td>
<td>Z</td>
</tr>
<tr>
<td>True retrieval</td>
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<td></td>
<td></td>
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<tr>
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<td>R</td>
<td>21</td>
<td>-4</td>
<td>-9</td>
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<td>30</td>
<td>-85</td>
<td>3</td>
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<td>-7</td>
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<td>L</td>
<td>-42</td>
<td>-43</td>
<td>-17</td>
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<td>High-confidence true retrieval</td>
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<td>L</td>
<td>-27</td>
<td>19</td>
<td>-18</td>
</tr>
<tr>
<td>Inferior Occipital Gyrus</td>
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<td>33</td>
<td>-88</td>
<td>0</td>
</tr>
<tr>
<td>Hippocampus/Amygdala</td>
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<td>-4</td>
<td>-9</td>
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<td>L</td>
<td>-6</td>
<td>-31</td>
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<td>-59</td>
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<td>-15</td>
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<td>-15</td>
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<td>R</td>
<td>53</td>
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<td>-59</td>
<td>-33</td>
<td>0</td>
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<tr>
<td>False retrieval</td>
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<tr>
<td>Middle/Superior Frontal Gyrus</td>
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<td>L</td>
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<td>12</td>
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<td>38</td>
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<td>R</td>
<td>18</td>
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<td>Conjunction (true &amp; false retrieval)</td>
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<td>47</td>
<td>L</td>
<td>-33</td>
<td>22</td>
<td>-5</td>
</tr>
</tbody>
</table>

The table reports areas distinctly activated for true retrieval (Remembered Hits) and false retrieval (Remember FAs) and areas that are common to both true and false retrieval. BA = Brodmann’s Area; H = Hemisphere; t = statistical t value; T&T = Talairach and Tournix coordinates.
False Greater than True Retrieval

On the other hand, false memories compared to true memories elicited greater activity in several frontal regions, including bilateral middle/superior frontal and dorso-medial PFC (dmPFC), and left superior temporal gyrus (see table 2).

Parametric Modulations: False Memories

Parametric modulation analyses were conducted to identify neural activity in regions that contribute not only to false memory for items related to studied items, but show a graded response as relatedness in the false alarm lures increase. As relatedness increased, increase neural recruitment was observed in bilateral middle temporal cortices, left anterior cingulate (ACC), and left superior frontal and vmPFC (see Table 3).

### Table 3. False alarm parametric modulation

<table>
<thead>
<tr>
<th>Area</th>
<th>BA</th>
<th>H</th>
<th>Coordinates (T&amp;T)</th>
<th>t</th>
<th>mm³</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ventrone-Medial Frontal Gyr</td>
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<td>-</td>
<td>6 52 7</td>
<td>6.03</td>
<td>6318</td>
</tr>
<tr>
<td>Middle Temporal Gyr</td>
<td>21</td>
<td>L</td>
<td>-53 -25 -8</td>
<td>4.75</td>
<td>1539</td>
</tr>
<tr>
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<td>R</td>
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<td>4.03</td>
<td>513</td>
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<tr>
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</tr>
<tr>
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<td>R</td>
<td>3 36 -21</td>
<td>3.26</td>
<td>270</td>
</tr>
</tbody>
</table>

The table reports areas that modulated false memories for the related lures. False alarm activity as relatedness increased and decreased. BA = Brodmann’s Area; H = Hemisphere; t = statistical t value; T&T = Talairach and Tournix coordinates.

Additional Results

Correct Rejection Parametric Analysis

In order to confirm that the regions identified in our parametric analysis were uniquely associated with false alarms activity and not due to relatedness more generally, we also investigated the parametric analysis in correction rejections as relatedness increase. In this analysis, one small cluster within the cerebellum was observed (see table 4).
Our *a priori* hypotheses predicted modulation for false alarms as relatedness increase in a series of regions, including prefrontal cortex, lateral temporal cortex, visual cortex (FFA), and MTL regions. While our results did in fact show that activity in frontal and lateral temporal cortices was modulated for false retrieval as relatedness increased, we did not see the predicted increases in FFA or MTL. In order to fully understand the response pattern within these regions, we took a closer look at activation within each respective ROI.

As a first step we used a functionally defined masked from our face localizer of bilateral FFA and an anatomically defined mask of bilateral MTL in order to further investigate false alarm activity within each region. For the FFA analyses, after obtaining a group-level FFA activity from our face localizer task (corrected at FDR .1 – reduced threshold), we used this activity as an ROI within the false alarm parametric contrast, also at a reduced threshold (p<.05 uncorrected). This allowed us to more closely observe the fine-grained involvement of the visual cortex (FFA) in false memories, as relatedness increase. Even at this reduced threshold, the FFA did not appear to be involved in the modulation of false memories, as relatedness increase. We also performed the above-mentioned analysis within the anatomically defined MTL ROI described above. There was also no significant activity within the MTL that appeared to modulate false memories, as relatedness increase. Furthermore, additional analyses that examined the overall pattern of activity for hits, misses, each level of false alarms and correct rejections also supported this finding. A repeated measure ANOVA revealed no significant results, for any of the above-mentioned contrasts of interests; mean

<table>
<thead>
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<th>Increased Relatedness</th>
<th>Cerebellum</th>
<th>--</th>
<th>L</th>
<th>-36</th>
<th>-64</th>
<th>-39</th>
<th>3.49</th>
<th>270</th>
</tr>
</thead>
</table>

The table reports areas that modulated correct rejections for the related lures. Correct rejection activity as relatedness increased. BA = Brodmann’s Area; H = Hemisphere; t = statistical t value; T&T = Talairach and Tournix coordinates.

**ROI results**
activity within each ROI did not appear to be modulated by the degree of relatedness in the false alarm lures (see figure 8).

**Discussion**

Using a modified version of the DRM/perceptual relatedness paradigm, the current study investigated the neural circuitry that mediates true and false memory retrieval as a function of the relatedness of the lures to the targets. As expected, our behavioral findings revealed a main effect of condition, showing that as perceptual relatedness increased, participants’ false alarms noticeably increased. This exemplifies that the perceptual relatedness of the lures, in reference to the target item, played an integral role in participants’ false alarm rate. Even though reaction time between the different levels of related lures did not show a significant linear effect for correct rejections, there was a linear main effect of reaction time for false alarms, as a function of relatedness. Additionally, because unrelated false alarms occurred at a significantly lower rate than the related false alarms, participants responded to the relatedness of the lures, with respect to the targets and not just a general likelihood of false alarming to new items.

The neuroimaging findings of our study are largely consistent with previous false memory literature (e.g., Garoff-Eaton et al., 2006; Slotnick & Schacter, 2004) in emphasizing the extensive overlap in the sensory and reconstructive processes that support both true and false recognition (Johnson, Hashtroudi, & Lindsay, 1993; Mitchell & Johnson, 2009; Schacter & Addis, 2009; Schacter & Slotnick, 2004). More specifically, both memory processes recruited common retrieval-related activity in left inferior and medial frontal gyrus, parietal cortex, and right inferior occipital cortex. Despite this overlap, direct comparison between true and false remembering revealed dissociations in the neural correlates mediating each type of memory. True compared to false retrieval elicited significantly greater activation in bilateral hippocampus/amygdala and visual regions, extending into the fusiform gyri (mainly left lateralized), as well as vmPFC, left superior and right inferior frontal gyri. In contrast, false compared to true retrieval exhibited greater activity in bilateral middle/superior frontal gyri, dmPFC, and
left superior temporal gyrus.

Finally, while previous studies treated relatedness (with respect to lures) in an all-or-none fashion, the current study examined false retrieval as a function of the degree of relatedness of the related lures compared to the targets. Results showed that a set of brain regions does in fact modulate false memories, as a function of relatedness. As relatedness of false alarms increased, greater neural recruitment was observed in bilateral middle temporal cortices, left anterior cingulate (ACC), and left superior frontal and vmPFC. Our results further clarify the roles of reconstructive and perceptual processes in false memories, as a function of increased relatedness. Each finding is discussed further, below.

*Common Activation Association with True and False Retrieval*

A conjunction analysis assessed neural regions that exhibited common activation across both true and false retrieval. In line with previous work, when collapsing across relatedness, we predicted that both memory processes would engage in similar object perception and identification processes to support overall episodic details to support identification of oldness. We also expected that both memory processes would engage highly similar retrieval-related evaluation and monitoring processes and decision-making that would be independent of accuracy. Both processes are also expected to be
mediated by a general feeling of oldness and familiarity, again, independent of retrieval accuracy, which would support the notion that both familiarity with a given stimulus and retrieval of episodic details are critical components of both memory processes.

The regions that have been implicated in such processes include regions within the visual cortex for overall object perception and identification, as well as regions within the frontal cortex for monitoring and decision-making. Insular cortex has also been shown to be connected with decision-making networks, including areas that are implicated in evaluation and response selection such as the anterior cingulate, DLPFC, and other prefrontal areas. Studies have also shown this region to be implicated in uncertainty in decision-making (Grinband, Hirsch, & Ferrera, 2006; Huettel, Stowe, Gordon, Warner, & Platt, 2006). Lastly, the parietal cortex has been shown to be involved in the overall sense of oldness and familiarity, independent of accuracy. Thus, we expect to observe common activity in the above-mentioned regions. Consistent with previous literature examining true and false recognition, this analysis revealed common retrieval-related activity in bilateral inferior and middle frontal gyri, insular cortex, parietal cortex, and occipital regions (see figure 4) (see Atkins & Reuter-Lorenz, 2011; Cabeza et al., 2001; Dennis, Bowman, & Turney, 2015 for review; Gutchess & Schacter, 2012; Kahn et al., 2004; Okado & Stark, 2003; Schacter, Buckner, et al., 1997; Slotnick & Schacter, 2004). Together, results show common activity between true and false memories within the core retrieval network. This overlap emphasizes general reconstruction, perceptual, and monitoring processes that were independent of the encoding history of the stimuli. Furthermore, the observed common activity in our study also suggests that our task was robust and able to identify the typical common retrieval-related network found in previous studies.

**True Greater than False Retrieval**

For true memories, more so than false memories, when collapsing across relatedness, we predicted that true memories would be associated with more sensory and perceptual details, compared to false memories. Also, having been encountered before, in line with the sensory reactivation hypothesis, true memories would elicit
reactivation of the encoding episode in sensory regions that were involved in their
initial encoding. The regions implicated in these processes include early visual cortex
and MTL as they have also been shown to represent accurate retrieval and
reconstruction of episodic details during retrieval. As expected, true compared to false
retrieval was mediated by a large network of brain regions including bilateral
hippocampus/amygdala and visual cortex (extending into the fusiform gyri), as well as
ventro-medial PFC (vmPFC), and left inferior frontal gyrus (see figure 5). These results
are in line with previous studies that investigated true recollection of semantic and
perceptual stimuli (Dennis et al., 2012; Henson, Rugg, Shallice, Josephs, & Dolan, 1999;
Slotnick & Schacter, 2004; Wheeler & Buckner, 2004; Yonelinas, Otten, Shaw, & Rugg,
2005).

Consistent with our predictions, our study provides supporting evidence for the
sensory reactivation hypothesis by showing greater activation in the early visual
regions (BA 18/19), for true compared to false retrieval. This visual activity also
extended into the fusiform gyrus, which is a region that has been shown to play an
important role in face processing, especially the recognition of familiar faces (Haxby et
al., 2000). Hence, its involvement in only the accurate retrieval of a face exemplified its
role in the recapitulation of item-specific details of the original face shown at encoding,
which in turn support the accurate retrieval of previously viewed faces. Thus, we
postulate that participants’ ability to accurately reconstruct item-specific details, which
helped distinguish between detailed retrieval of true, compared to false memories, was supported by the observed activity in these regions.

As expected, MTL activity represented accurate retrieval and reconstruction of episodic details of information that was presented at encoding. Additionally, having been previously encountered, items are expected to be more salient and relevant to the participants. Amygdala activity has been attributed to general emotional processing, such as detection or attribution of salience (Liberzon, Phan, Decker, & Taylor, 2003). This region has also been shown to be involved in orchestrating appropriate responses and processes (i.e., perceptual, attentional, cognitive/conceptual) to relevant information (Cunningham et al., 2012). In our study, this activity provides insight to show that the amygdala, at least in part, is a part of a larger network that informs one about what is relevant in one's environment.

In addition to MTL and visual activity, we also observed increased activity in several PFC regions, including ventromedial PFC (vmPFC), left inferior frontal gyrus (VLPFC), for true greater than false memories. We predicted that true memories would be accompanied by episodic details, in this case, with the help of conceptual frameworks. The vmPFC has been shown to play a crucial role in the encoding and consolidation of new information (Frankland & Bontempi, 2006; Takashima et al., 2006; Wang & Morris, 2010). Particularly, the this region has been shown to facilitate the integration of information into existing schematic/conceptual frameworks when information shares similar characteristics to prior information (van Kesteren, Ruiter, Fernández, & Henson, 2012), successfully utilizing schematic memory (Tse et al., 2007; van Kesteren, Fernandez, Norris, & Hermans, 2010; Wang & Morris, 2010; Warren, Jones, Duff, & Tranel, 2014). Other studies also indicate that the hippocampus and vmPFC both play important roles in updating existing memories through retrieval-mediated learning (Tse et al., 2007; Zeithamova, Dominick, & Preston, 2012). Moreover, studies show that the vmPFC is anatomically (Ongur & Price, 2000; Saleem, Kondo, & Price, 2008) and functionally (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Ranganath, Heller, Cohen, Brozinsky, & Rissman, 2005) connected with MTL.
regions to support memory. Thus as predicted, this activity would represent the accurate retrieval of items that fit into the schematic framework that was established at encoding.

We also observed activity within left ventro-lateral PFC (VLPFC). While associated with many functions, VLPFC has been shown to resolve interference between items that share semantic properties (Atkins & Reuter-Lorenz, 2011; Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005). In our study, such frontally mediated control processes were critical to dissociating old faces from the related lures, given that they share properties with studied faces. Another study by Thompson-Schill and colleagues (1997) found left VLPFC involved in the selection of available information midst competing options. This mechanism is part of a more general PFC system that is required for the selection of responses from memory. Collectively, these results suggest that true retrieval was mediated by recapitulation, accurate reconstruction, and evaluation of item-specific details of the encoding event.

**False Greater than True Retrieval**

On the other hand, false compared to true retrieval was expected to be based on more gist or relatedness processing and require more evaluation and monitoring. Unlike true memories that are accompanied by the recapitulation of sensory details, false memories are often believed to be evoked from familiarity of a related lure in the absence of encoding-related details (Cansino, Maquet, Dolan, & Rugg, 2002; Yonelinas et al., 2005). Therefore, making a memory decision in the absence of such details has been posited to require greater monitoring and evaluation than when one has access to supporting details. This will also then lead to increased task difficulty. These processes have been associated with frontal regions for monitoring, evaluation, and task difficulty (Cabeza et al., 2001; Garoff-Eaton et al., 2007; Kensinger & Schacter, 2006; Kim & Cabeza, 2007c; Kubota et al., 2006; Okado & Stark, 2003; Schacter, Buckner, et al., 1997; Schacter, Savage, et al., 1996; Slotnick & Schacter, 2004) and superior/middle temporal gyrus for gist processing. As a result, we expect to see increases in these regions.
As predicted, false compared to true retrieval was accompanied by increased activity in several frontal regions, including bilateral middle/superior frontal gyri, dorsal medial PFC (dmPFC), and left superior temporal gyrus (see figure 6). Increased activation in the above-mentioned frontal regions, during false memories, is consistent with previous studies that examined false retrieval of semantic and perceptual stimuli (Cabeza et al., 2001; Goldmann et al., 2003; Henson et al., 1999; Schacter, Koutstaal, Johnson, Gross, & Angell, 1997; Schacter, Savage, et al., 1996; Slotnick & Schacter, 2004; Wheeler & Buckner, 2004; Yonelinas et al., 2005).

![Figure 6. Regions showing greater activation for false compared to true retrieval, including (a) left superior temporal gyrus, (b) bilateral middle/superior frontal/ACC.](image)

Also in line with our predictions, false greater than true retrieval, exhibited activation in the left superior temporal cortex, a region associated with semantic processing and semantic gist. Language research has associated activity in the left middle and superior temporal gyrus to semantic gist (for reviews, see Thompson-Schill et al., 2006; Kable et al., 2002; Wise and Price, 2006; Dennis et al., 2008b, 2007b). Supporting the role of this area in processing semantic gist, patients with semantic dementia (and damage to this region) are impaired at extracting and/or utilizing semantic gist (Simons, Verfaellie, et al., 2005). Additionally, within the context of false memory, Dennis and colleagues (2007b, 2008, 2012, 2014) consistently found that this region supported both semantic and perceptual false memories in which there was a shared semantic component (e.g., semantic: studying pig, cow, sheep, and goat and view
horse as a lure; perceptual: studying 8 exemplars of a given category (dogs, flowers) and presented with new exemplars from the same category at retrieval). The researchers interpreted this activation as evidence of semantic processing associated with a specific category or integration of a category along with its exemplars that supported subsequent retrieval by providing individuals with a strong representation of semantic gist on which to base their memory decisions. Thus, as expected, increased activity in the left superior temporal gyrus reflected an increased reliance on gist processing for false memories, compared to true memories.

Interestingly, the role of the middle/superior temporal cortex has been observed in previous studies that utilize combined semantic and perceptual paradigms. In the current study however, because we used a purely perceptual paradigm with a set of stimuli that had a single category label (faces), this finding is rather thought provoking. Possible explanations are that (1) this region may represent gist processing more generally and/or (2) there was still some semantic processing involved, supporting false retrieval of face lures. Specifically, perhaps participants still engaged in some semantic labeling during the encoding of a given face that lead to the retrieval of the label in the presence of a related lure. For instance, when a familiar (not true target face) face was encountered, it is probable that participants used a semantic label such as “the girl with the dimple on her chin” to assist with such encoding and that is what is brought to mind at retrieval. This would be especially relevant to the retrieval of these false memories, as they are not accompanied by the recapitulation of sensory details, as in true memories. This finding suggests that the contribution of the left lateral temporal cortex may play a more general role in false memories. In future research it will be interesting to see whether activity in this regions also supports false memories that cannot rely on any semantic labeling.

*Parametric Analyses: Increases in Activity for False Memories as Relatedness Increases*

One of the main goals of the current study was to examine the role of systematic increases in perceptual relatedness in false memories on neural recruitment. As the similarity between the related lure and the target increase, we expected an increase in
various processes, including decision-making. One can imagine distinguishing between a 70:30 morph and the target face would require greater demands that say a 50:50 or a less related or completely unrelated face. Thus, we expected response conflict between the lures and the internal representation of the target item; as the similarity between lures and the target increase there is increase in conflict and difficulty in decision-making.

Behavioral studies also propose that the processes that underlie false recognition are increasingly engaged as more related information is encountered (Koutstaal & Schacter, 1997). Thus, we predicted that as the face becomes more and more similar to a face seen at encoding, due to the perceptual or conceptual overlap, conceptual/perceptual gist of the faces would increase, which would lead to greater false memories. In line with this, our findings would be consistent with the Fuzzy Trace Theory, which posits that false recognition is mediated by a strong sense of familiarity and often predicated on retrieval of the gist trace (Deese, 1959; Reyna & Brainerd, 1995). Regions involved in these processes include the frontal regions, for example, the DLPFC for decision-making and task difficulty and middle and superior temporal cortex for relatedness processing. Therefore we expect to observe a graded response in these regions.

As predicted, we observed that as the similarity between the related lure and the target increased, activity within bilateral middle temporal cortices, left anterior cingulate (ACC), left superior frontal and vmPFC also increased (see figure 7). This analysis extends the previous false greater than true analysis and prior research in the false memory domain as it goes beyond examining false memories in an all-or-none fashion. The results of this parametric analysis are novel as they provide information regarding the response of several brain regions, across differing levels of relatedness within the context of false memory retrieval.

As mentioned earlier, the left lateral temporal cortex has been implicated in language and semantic processing. Accordingly, in our study, this increased activity for false greater than true retrieval proposes that semantic and possibly perceptual gist traces
(general memory for a face at encoding) contributed significantly to false memories. With regard to activity within the left superior frontal cortex and ACC, as noted above this region is associated with task difficulty and decision-making. False memory studies have attributed increased ACC activity to increased effort (Garoff-Eaton et al., 2006; Okado & Stark, 2003; Slotnick & Schacter, 2004) difficulty of making a response decision (Maril, Wagner, & Schacter, 2001), as well as greater mnemonic processing of the related lures (Iidaka et al., 2012; Okado & Stark, 2003; von Zerssen et al., 2001). Other studies examining conflict between competing representations (Barch et al., 2001; van Veen & Carter, 2002) and competing mnemonic representations (Kuhl et al., 2007) also attribute increased ACC activity to the handling of such increasing cognitive demands. As a result, we predicted that a graded response observed in these regions (i.e., increased activity as the relatedness amongst the related lures increased) would reflect the response conflict between the lures and the internal representation of the target item. This would also suggest an increase in conflict and difficulty in decision-making as the similarity between lures and the target increase. Specifically, we expected that as the related lures became more similar to the target, it would be more difficult to decide whether a face was old or new. As predicted, increased activity in several frontal regions, including ACC represented increased difficulty and decision making, as relatedness increased.

As the face becomes more and more similar to a face seen at encoding, familiarity to the encoded face is expected to increase. Therefore, the regions within the
extended face-processing network associated with processing familiarity/episodic memories should also increase in a graded fashion (vmPFC and Posterior cingulate cortex). Previously in our true greater than false retrieval, vmPFC reflected the integration of information into existing conceptual frameworks from encoding along with its involvement with the hippocampus to support memory retrieval. However, it seems logical that this would also hold true for our false parametric analysis. Specifically, as the faces become more and more familiar to the target face, the increased relatedness between the lures would demand more decision-making and monitoring and this can be aided with the help of conceptual frameworks. Yet, because false memories are not accompanied by sensory details, as are true memories, the use of conceptual frameworks (schemas) to retrieve memories will likely lead to false memories. For instance, increasing the relatedness of the lures to the targets increases gist traces, which in turn increases the probability of false memories. In line with previous work, the observed vmPFC in our study may serve as a neural substrate for these processes, showing that vmPFC could reflect the weighting of different options during complex decision-making (Damasio, 1994; Bechara et al., 1997; Bechara and Damasio, 2005; Koenigs et al., 2007). This provides some insight into how the role of information integration through conceptual/schematic frameworks influences false memories for related information.

One may speculate that the foregoing findings reflect activity associated with decision-making and/or relatedness more generally and are not specific to false memory activity. In order to explore such hypothesis, we also examined the activity that parametrically modulated correct rejections. At the threshold used in the current study, (p<.005), results revealed only one small cluster of activity within the cerebellum (see table 4). Additionally, we used this activity that was associated with correct rejections (at a liberal threshold of p<.05) as an exclusive mask on the false alarm parametric analysis. This threshold of p<.05 was quite conservative as an exclusive mask. Again, no region overlapped between the two analyses. Thus, we conclude that none of the regions evident in the false alarm relatedness parametric contrast were present for correct rejections, as relatedness increased. Taken together, results suggest that the
regions identified in the false alarm parametric analysis are not simply modulated by general relatedness, but instead reflect increases in activity that is specific to false memories.

While the parametric analysis identified predicted increases in PFC, it failed to find activation within the MTL and the FFA. We expected to see a linear increase in these regions, as relatedness increased because of their role in reconstruction and the tracking of relatedness (MTL) and the processing of faces (FFA). In order to fully interrogate these two regions of interest we performed ROI-based analyses (as described above). Even at a more liberal threshold (p<.05), results revealed no significant increases in activity as a function of relatedness for either ROI. As an additional exploratory step we plotted activity in each ROI as a function of each level of relatedness within false alarms (i.e., 70/30; 50:50; 30:70; 0:0 activity) in order to visualize any pattern of activity across relatedness within each ROI. Our results revealed (Figure 8) no systematic pattern in the FFA or MTL.

The FFA is known to be involved in the recognition of familiar faces (Haxby et al., 2000). Nevertheless, within the context of false memories, this region does not appear to modulate related false memories (as faces become more and more familiar or similar to target faces). This can be interpreted as the FFA having preference for true old faces. In this case, it would appear that the lure face, even if very related to the target face, was not sufficient to elicit activity from the FFA region. Furthermore, this FFA ROI was evident for true greater than false memories and not for false greater than true memories. This provides further support for the involvement of the FFA for truly old faces, showing its involvement in the processing of retrieving item-specific details, which supports true memories.
As for MTL activity, this region has been implicated as a region that tracks relatedness to support true memories (Cabeza et al., 2001; Dennis et al., 2012; Dennis et al., 2008b; Giovanello, Kensinger, et al., 2009; Kahn et al., 2004; Kensinger & Schacter, 2006; Kim & Cabeza, 2007c; Paz-Alonso et al., 2008). We originally hypothesized that the inconsistency of MTL findings for false memories may have been due to the lack of a systematic measure of the related lures used across studies. Yet, even in our study, MTL still did not appear to modulate activity of related false memories. This could be interpreted similarly to that of the visual (FFA) activity above in showing that though the MTL may be involved in the reconstruction and retrieval of sensory details, in false memories, unless the details are truly old, they are not tracked throughout this region. In saying so, it is also possible that only parts of the MTL track relatedness (i.e., PHG, anterior vs. posterior parts of the hippocampus, etc.). Future studies should examine this more closely as it can provide great details into the reconstructive processes.
involved in false memory retrieval.

All in all, this analysis produced some interesting findings, showing that many of the same relevant processes, as well as a different set of regions respond in a graded fashion, as relatedness increase. Thus, our results provide great insight into our understanding of false memories, suggesting that the reliance on familiarity and relatedness traces are fundamental to the creation of false memories (Brainerd & Reyna, 2002; Dennis et al., 2008; Dennis et al., 2008b; Koutstaal & Schacter, 1997).

Limitations and Future Directions

The present study was able to replicate previous findings of common and distinct activity of true and false memories. Moreover, we were able to better understand role of relatedness in false memories by systematically varying relatedness. Nevertheless, there are some limitations to our approach. For example, it would also be very informative and beneficial to the literature if future work would also examine these processes during encoding. This will help us understand the neural mechanisms that also lead to the formation of these false memories and assess activity that leads to false memories depending on how different the lure is from the original item representation.

Additionally, we identified several findings contrary to our predictions, such as the lack of early visual cortex activity associated with our false memory parametric analysis. Given that the current study is one the first and only study to systematically measure relatedness across the related lures, we realize the need for more research within this domain, using similar paradigms. Additionally, while we discuss the results in terms of relatedness in false memories, we recognize that replication across varied stimuli (other than faces) is needed. Future work in the domain of systematic relatedness will hopefully replicate the present study’s findings as well as provide stronger support for the role of vmPFC and lateral temporal cortex in tracking false memories as a function of relatedness. Investigating the role and more specific
distinction of these regions in related false memories will be fundamental to understanding the mechanisms that mediate false retrieval.

Another caveat may be the limited power between our false alarms, correct rejections, hits, and misses. Specifically, the average number of trial types in our hits and misses (as shown in table 1), are much greater than that of false alarms and correct rejections. This was due to the difficulty of having enough trials in each level of relatedness. While we recognized this from the outset and it is the reason why we both a) collapsed false memories across each relatedness category and b) used a parametric analysis to examine relatedness within false memories, we note that future studies should adjust task design to better account for this imbalance. This approach will also allow closer exploration of the mechanisms involved in true and false recollection.

One may also stipulate that some of our findings are influenced by template matching, the direct comparison of incoming sensory information to identical copies (templates) stored in memory. Though our study is unable to directly refute this assumption, we can say that based on the sensory reactivation hypothesis, the regions involved in true greater than false retrieval are in support of previous well-established studies. Nevertheless, future studies should examine this more closely, using a template-matching paradigm and examine whether the same regions involved in the encoding of the templates reactivates during matching. Overall, this line of research and/or paradigm should be expanded to more stimuli types beyond faces, including objects (i.e. morphed) as well as semantic analyses of words to ensure the involvement of semantic processes in false memories. This will provide great insight into the role of gist processing in false memories, as well as help us better understand the function of various regions, as a function of relatedness.

**Conclusion**

The current study aimed to elucidate the cognitive mechanisms and neural correlates underlying both true and false retrieval, as well as the influence of systematic relatedness of lures on false retrieval. Our results converge with previous studies in
that true and false memories engage many of the same regions, when collapsed across relatedness. Furthermore, we replicated previous research with respect to distinct neural activity supporting true and false memories. Specifically true greater than false memories showed increased activity in bilateral hippocampus/amygdala and visual regions while false greater than true memories elicited increased activity in left middle/superior frontal, dmPFC, and left superior temporal gyrus. Altogether, our study found true memories, compared to false memories, to be associated with regions involved in evaluation, accurate reconstruction, and recapitulation of item-specific details of the encoding event. Hence, it can be assumed that the faces correctly remembered were processed on a more item-specific level. In contrast, relatedness processing, monitoring, and decision-making regions accompanied false memories, suggesting the strong involvement of relatedness processing.

Unique to our study, we also examined the role of systematic increases in perceptual relatedness/similarity in false memories on neural recruitment supporting false memories. Results revealed many perceptual and constructive processes that contribute to false memories, identifying unique regions within the false retrieval network that modulated related false memories, as a function of relatedness. Results further clarified the role of the prefrontal and lateral temporal cortex with regard to their support of false retrieval, showing that as similarity between the related lures increased, activity throughout these regions also showed a graded response. Collectively, results provide great insight into understanding the computational processes of different regions within the false memory network. Results also provided a better understanding of the development of false memories that are based on the retrieval of relatedness or gist-based information. Consequently, this study advanced our understanding of how false memories can arise from otherwise adaptive cognitive processes.
References


