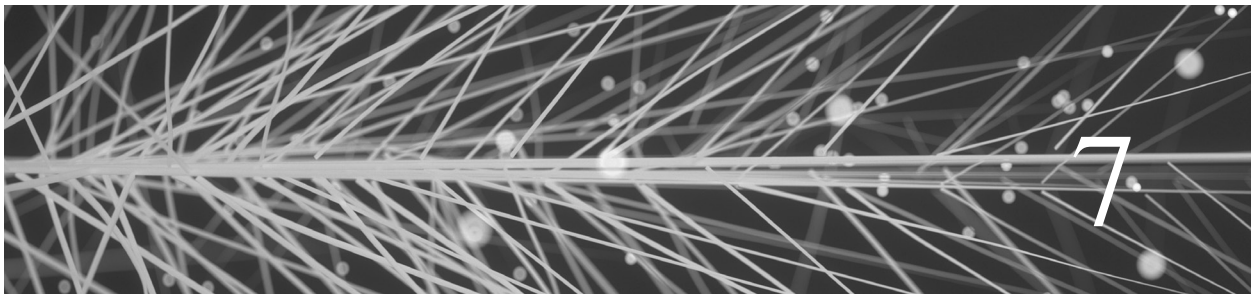

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False Memories: What Neuroimaging Tells Us About How We Misremember the Past

Nancy A. Dennis, Jordan D. Chamberlain, and Catherine M. Carpenter

INTRODUCTION

Every memory researcher will tell you that memory retrieval does not function like a tape recorder. Rather, memory retrieval is fallible and prone to inaccuracies. A false memory is a memory error that occurs when one remembers a past experience in a manner that is inconsistent with the way in which the event originally occurred. This could involve mistaking details within the event, erroneously recombining details across previous events, or even retrieving a partial or full false memory for an event that never occurred before. Examples include cases of eyewitness testimony in which eyewitnesses report that someone committed a crime in which they were never involved, or thinking that you took your medicine when you never did. Additionally, one may falsely remember the name of an acquaintance while at a social function or outside the context in which that acquaintance is normally seen (i.e., the butcher on the bus; Mandler, 1980).

While previous chapters and reviews (e.g., Dennis et al., 2015; Kurkela and Dennis, 2016) have summarized neural activity that both overlaps with, and differentiates between, true and false memories, the current chapter will offer several novel insights into the neural processes underlying false memories with respect to univariate and multivariate neuroimaging methods. First, we will summarize new support for previously observed patterns of false memory activity across the cortex. We will expand this past summary of BOLD activation to also include results from recent advances in analytical methodologies, including multivoxel pattern analysis (MVPA) and representational similarity analysis (RSA), including encoding-retrieval similarity analyses (ERS). Finally, we will examine how structural components of neural architecture relate to false memories and how neural processes underlying false memories differ in aging.

We first review the most common paradigms that investigate false memories in order to provide the groundwork for understanding the neuroimaging results. We then review findings from both encoding and retrieval memory phases, and studies that examine the correspondence of neural activity across the two memory phases. Within each section we draw interim conclusions regarding cognitive and neural processes involved in the commission of false memory errors with respect to each processing step. Parallels across findings are highlighted. We conclude with an overview regarding how the neural processes identified in

younger adults differ in aging, where increased false memories are a ubiquitous finding. Finally, in line with the aims of the chapter, we will offer an overarching perceptive on the totality of the evidence to date regarding processes that lead to false memory errors, including areas for future investigation.

FALSE MEMORY PARADIGMS

Within the literature, false memories have been studied using a variety of methodological approaches. The most common methods have included the use of related word lists to study semantic false memories, perceptually similar objects to study visual false memories, misinformation paradigms to study the effects of misleading information on false memories, and associative memory paradigms to study source errors. While each paradigm is unique and approaches the study of false memory from a slightly different perspective, the findings from neuroimaging investigations of memory errors across paradigms are relatively consistent. This consistency has allowed researchers to draw convergent interpretations regarding the mechanistic foundation of false memory errors, and advance predictions about the relationship between veridical and false memories. Let us first review the paradigms themselves.

With its foundation within the DRM (Deese-Rodeiger-McDermott) paradigm (Deese, 1959; Roediger and McDermott, 1995), semantic false memories represent one of the oldest researched false memories. In traditional semantic memory paradigms, individuals are given lists of related words to study (e.g., "bed", "rest", "awake", "tired", "dream", "wake", "snooze", "blanket", "doze", "slumber", "snore", "nap", "peace", "yawn", and "drowsy") and then tested on memory for a related lure, in this case, "sleep". Although "sleep" is not presented among the list of studied words, individuals often falsely recall and/or recognize this related lure during a memory test. Among the several theories that have been posited to account for semantic false memories is that of spreading activation (Roediger et al., 2001) and gist-based processing (Brainerd and Reyna, 1990, 2002). The spreading activation theory proposes that our memory for individual items is stored as single units of information and that these units are connected to form semantic networks of related concepts. According to this model, retrieval of one of the units occurs by activation spreading across the network, including the critical lure or concept, with such activation of that lure item supporting false memories (Roediger et al., 2001). The fuzzy trace theory, on the other hand, posits that a false memory for the related lures arises due to the encoding and subsequent retrieval of a gist-based representation of the encoded event (in this case, all the semantically related words). When a related lure shares the same gist as that which was encoded, retrieval of a gist trace, absent of verbatim information, leads to the erroneous endorsement of the lure as "old" (Brainerd and Reyna, 1990, 2002).

False memories have also been studied in the perceptual domain, wherein memory errors are made when an individual incorrectly endorses a new (or lure) item that is perceptually similar to that which was previously presented. Such perceptual memory errors are most often explained using the gist-based account described above, wherein general perceptual (e.g., shape, color) or semantic properties (e.g., semantic label; Oliva, 2005) are utilized during memory retrieval in lieu of more detailed mnemonic information. Furthermore, in the presence of overlapping perceptual information, as in the case with physically similar lure items, individuals may fail to neurally distinguish between the similar representations, engaging not in pattern separation, but pattern completion processes when viewing the lure item (e.g., Yassa et al., 2011; Yassa and Stark, 2011), thereby endorsing the lure as "old" based on this overlap.

Relatively distinct from the single item errors described above, false memories from misinformation typically arise when an individual does not retrieve the original details of a given event, but erroneously remember subsequently presented (mis)information instead. Misinformation-based false memories are thus similar to associative and source memory errors that occur when the combination of event details is erroneously rearranged or misattributed in memory. For example, one may remember meeting "Sawyer", but believe they encountered her in the grocery store, when they actually met her at the bank. Similarly, in an association memory task, one may be presented with the following word pairs: "blanket-soda" and "wallet-tree" and subsequently remembering "blanket-tree". What makes the foregoing situations particularly vulnerable to memory errors is that all queried information was presented during study or at some point prior to test, lending a high degree of familiarity to the misinformation, source, or individual components of the new paired associate. Thus, like semantic and perceptual false memories, there is a basis for the false memories that arise directly from the encoding episode.

RETRIEVAL

The majority of neuroimaging work examining false memories has focused on retrieval-related processing that corresponds to the occurrence of the memory error itself. In doing so, studies have been able to both assess similarity of neural processing associated with the correct endorsement of a target and the incorrect endorsement of a lure, while also probing for differences between the two trial types. Similar comparisons are also made looking across correct and incorrect responses to the lure itself (i.e., a correct rejection vs. a false alarm). In doing so, univariate studies focus on the comparison of overall activation levels (i.e., BOLD signal) and location of neural activation between false and veridical retrieval. The most consistent finding within this line of research is that of large-scale neural overlap in activation between true and false memories, extending to much of the retrieval network. Such overlap has been observed within bilateral frontal and parietal regions (Atkins and Reuter-Lorenz, 2011; Beato et al., 2012; Boldini et al., 2013; Dennis et al., 2012; Iidaka et al., 2012; Kahn et al., 2004; Liu et al., 2020; McDermott et al., 2017; Schacter et al., 1997; von Zerssen et al., 2001; Webb et al., 2016), bilateral caudate and insula (McDermott et al., 2017; von Zerssen et al., 2001), lateral temporal cortex (Cabeza et al., 2001; Garoff-Eaton et al., 2006; McDermott et al., 2017; Turney and Dennis, 2017; Webb et al., 2016), and ventral visual regions (Dennis et al., 2012; Iidaka et al., 2012; McDermott et al., 2017; Slotnick and Schacter, 2004; Stark et al., 2010; Turney and Dennis, 2017; von Zerssen et al., 2001; Webb et al., 2016). Included in this overlap is activation across core memory regions with the medial temporal lobe (MTL), including the hippocampus and parahippocampal gyrus (PHG) parahippocampal gyrus (PHG) (Cabeza et al., 2001; Dennis et al., 2012; Garoff-Eaton et al., 2006; Gutchess and Schacter, 2012; Jeye et al., 2017; Kahn et al., 2004; Liu et al., 2020; Schacter et al., 1996a; Schacter et al., 1997; Slotnick and Schacter, 2004; Stark et al., 2010; Turney and Dennis, 2017; von Zerssen et al., 2001; Webb et al., 2016) (Figure 7.1).

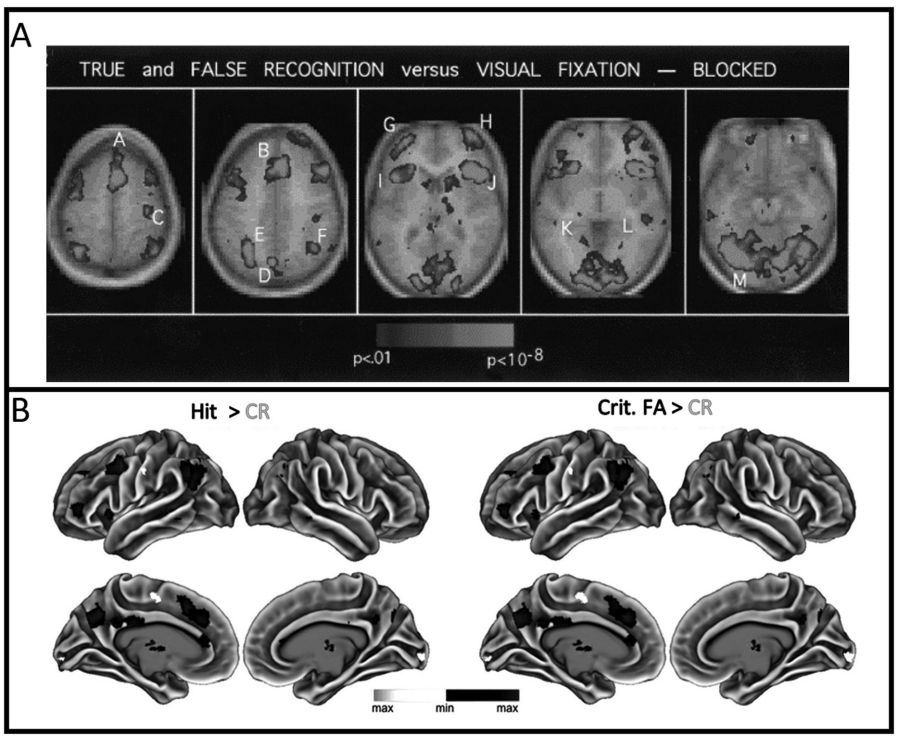

Figure 7.1 Common neural activity for true and false memories throughout frontal, parietal, temporal and occipital cortices. (A) adapted from Schacter et al., 1997; (B) adapted from McDermott et al., 2017.

The finding that retrieval of false and veridical memories involves largely the same set of neural substrates is reflective of both the similarity in the properties of both targets and lure items, as well as processing across the two types of stimuli during the retrieval process—that is, at a stimulus level, target and lures within a given memory paradigm are highly similar in both physical attributes (e.g., shape, color, form) and mnemonic properties (e.g., semantic labels, common contextual sources). As such, the simple act of processing either stimulus engages a common set of neural processes. Whether the memory decision results in an accurate or inaccurate assessment of the stimulus at retrieval likely depends on the amount and quality of encoded information subsequently retrieved, and the emphasis placed upon different aspects of the retrieved information during the evaluation and decision process (for more on this point, see below). While targets and lures may be processed within the same sensory "space" (i.e., occipital and auditory cortices), the manner by which each type of stimuli may differ.

To this point, one of the most common findings regarding veracity differences in false memory research is the sensitivity of sensory regions for detecting differences between veridical and false memories. Using univariate methods, numerous studies have found that activity is often stronger for veridical as compared with false memories within (e.g., Schacter et al., 1996b) and ventral visual regions, specifically early visual regions in which perceptual properties are presumed to be reinstated at retrieval (Abe et al., 2008; Dennis et al., 2012; Karanian and Slotnick, 2014, 2017; Slotnick and Schacter, 2004; Stark et al., 2010; Turney and Dennis, 2017) (Figure 7.2). This idea is encapsulated in the "sensory reactivation hypothesis" which first originated from early neuroimaging work that investigated spatial overlap across memory processing stages (Marche et al., 2010; Mather et al., 1997). The notion being that, reflective of a targets' prior history and encoding, which is absent for lure items, targets will evoke access to more sensory-related details from the encoding episode than a lure that has not been previously encountered. The relative strength of this sensory activation (e.g., false recollection, Dennis et al., 2012), suggesting that such sensory differences are not related to perceived strength of the memory alone. (Dennis et al., 2014; Fabiani et al., 2000; Gonsalves et al., 2004; Karanian and Slotnick, 2014).

Recent work from our lab, using MVPA, supports this earlier work showing that patterns of neural activation associated with target and lure items are discriminable within occipital regions (Bowman et al., 2019; see also Lee et al., 2019). However, this neural sensitivity also appears to be dependent on the degree of perceptual similarity between targets and lures. For example, we found that neural patterns throughout the ventral visual cortex, including middle occipital cortex, lateral occipital cortex, fusiform, and inferior temporal cortex, were able to distinguish between targets and lures when they differed in both perceptual details and a semantic label. However, only middle occipital cortex was able to differentiate between retrieval items when they differed on perceptual details alone (Figure 7.3). Furthermore, neural discriminability in middle occipital cortex positively predicted behavioral discriminability (indexed by d') across our sample of young and old adults. Such findings suggest that more differentiated neural patterns contribute to successfully determining whether a retrieval item is indeed old or new. Findings from the foregoing studies strongly suggest that the processing and retrieval of item-specific details within primary sensory cortices is a critical component of memory success, especially when novel information is perceptually related to studied information.

While the above findings have been interpreted as reflecting the strength of item-specific details supporting veridical memories, the strength of gist traces in memory retrieval has been found to have an opposite effect on memory accuracy—that is, work from our group has found that greater neural activity in the middle temporal gyrus (MTG; Noppeney et al., 2007; Price, 2000; Simons et al., 2005; Wise and Price, 2006) exhibits increasing activity as conceptual and perceptual lure items become (Turney and Dennis, 2017; Webb et al., 2016). Extending this work to semantic memories Chadwick et al. (2016) found that the similarity of neural patterns within the left temporal pole between encoded words and their respective concept (i.e., "bed," "pillow," "dream," with "sleep") positively corresponded to rates of false memories in a DRM paradigm. The analyses further showed that an individual's unique neural representations within the temporal pole predict their specific pattern of false-memory errors. The authors attributed this increased neural similarity to greater semantic processing. Put another way, less differentiated encoded semantic information appears to contribute to false memory processes. Such findings suggest that participants rely on the semantic or perceptual gist when making their memory decisions regarding related lures to the detriment of behavioral performance. Related, Gutchess and Schacter (2012) found that high levels of gist (as measured by the size of the encoding stimulus) led to reduced visual activity and increased false memories. The authors interpreted this finding as indicating that true memories rely on parsing

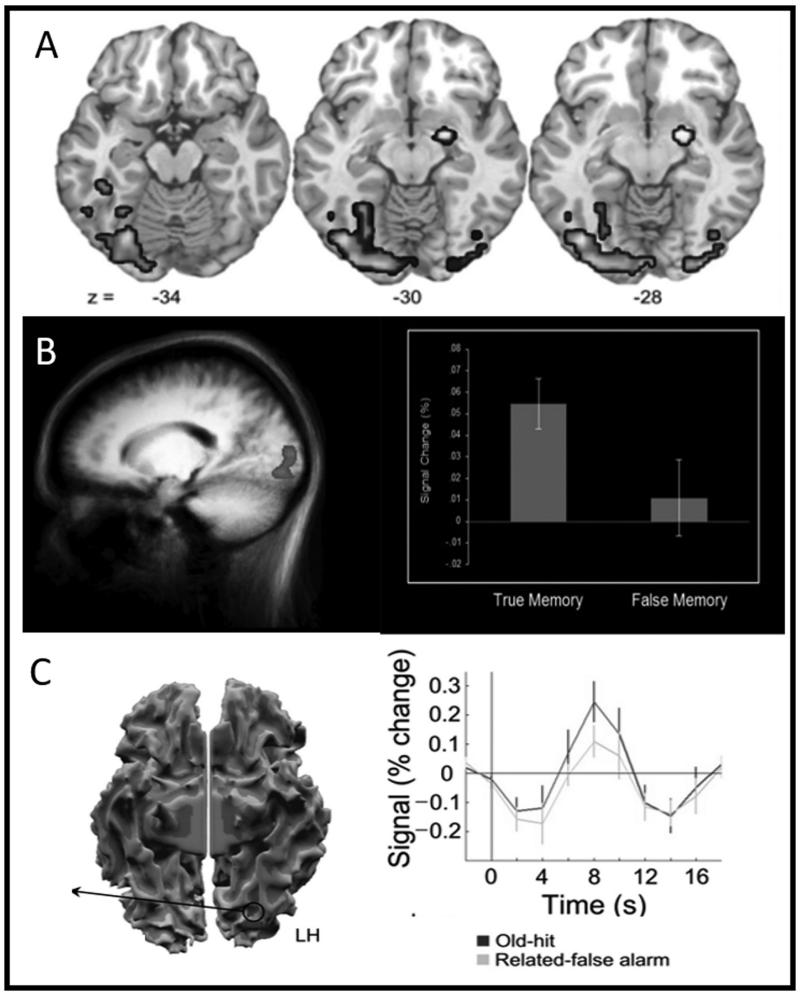

Figure 7.2 Activity supporting sensory reactivation hypotheses, whereby true memories evoke greater activity in early and late visual cortices during retrieval. (A) adapted from Turney and Dennis, 2017; (B) adapted from Karanian and Slotnick, 2017; (C) adapted from Slotnick and Schacter, 2004.

individual perceptual features and that this may be best supported under low gist conditions (Lee et al., 2019; Ye et al., 2016).

In addition, false memories have shown to be associated with increased activity in frontal-parietal cortices, irrespective of the source of the false memory (i.e., semantic, perceptual, source error). This increase in PFC and parietal activation has been identified when comparing false memories to accurate memory responses, both in the form of true memories and correct rejections (Cabeza et al., 2001; Garoff-Eaton et al., 2007; Kim and Cabeza, 2007b; Kubota et al., 2006; Okado and Stark, 2003; Schacter 1997a; Schacter et al., 1996a; Slotnick, 2004; Stephan-Otto et al., 2017; Turney and Dennis, 2017; Webb et al., 2016), with more recent work also showing that parietal cortices can reliably discriminate between patterns of activation associated with false memories and correct rejections (Lee et al., 2019). While the foregoing studies have noted increased activation across much of the frontoparietal cortex, a recent meta-analysis recently identified the peak of this activation as being focused within the medial superior frontal gyrus and inferior parietal cortex (Kurkela and Dennis, 2016). Noted in studies of memory

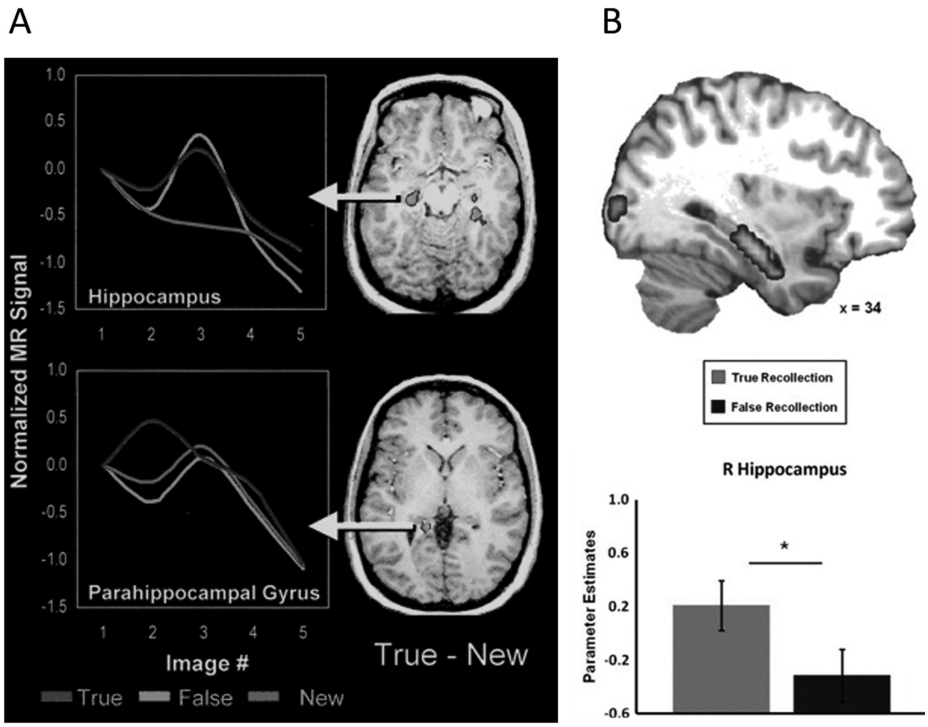

Figure 7.3 MTL activity during true and false memory. (A) The left anterior hippocampus shows common activity for both true and false as compared with new items (upper panel), whereas the left posterior PHG shows increased activity only for true memories (lower panel) (adapted from Cabeza et al., 2001). (B) Activity in right hippocampus shows greater activity for true as compared with false recollection (adapted from Dennis et al., 2012).

retrieval and cognitive control, the fronto-parietal network and specifically the medal superior frontal gyrus has been shown to play a critical role in evaluation and monitoring of difficult memory decisions (Ray et al., 2020; Sestieri et al., 2017; Wheeler and Buckner, 2004). The foregoing findings suggest that false memories may be distinct from veridical memories with respect to the extent and depth of evaluation that is needed prior to endorsing the lure as "old" (compared with a similar response made to a target item). In particular, we have noted that added evaluation and monitoring of retrieval traces is likely necessary when item-specific information is lacking. As such, the findings across visual and frontal cortices may correspond to the amount and content of detailed information retrieved (Gutchess and Schacter, 2012; Ye et al., 2016).

While several studies have identified MTL activity associated with false memory retrieval (Cabeza et al., 2001; Dennis et al., 2012; Jeye et al., 2017; Kim and Cabeza, 2007b; Schacter et al., 1997a; Stark et al., 2010; Turney and Dennis, 2017; Webb et al., 2016), the typical finding is that this activity does not supersede that which is observed for true memories. Nor have studies shown MTL activity to correspond to rates of false memories. Yet more recent work has suggested that the co-activation of MTL and cortical regions might be critical in understanding how MTL processing underscores false memories (Carpenter et al., 2021; Wing et al., 2020). For example, Carpenter et al. (2021) found that increased neural pattern similarity associated with incorrect context reinstatement in inferior temporal gyrus mediated the relationship between hippocampal BOLD activation and false memory effects. Such effects suggest that hippocampal processes may contribute to overlapping information in inferior temporal gyrus. Univariate work by Jeye et al. (2017) found that BOLD estimates of false memories were negatively correlated between anterior prefrontal cortex and hippocampus, such that participants with greater hippocampal activity also exhibited reduced frontal activity.

The implication is that as detailed information retrieved from the hippocampus is reduced, greater frontal monitoring resources are needed to reach a memory decision, often resulting in a memory error. Taken together, results suggest that the MTL may not act alone in contributing to false memories, but it may be the lack of MTL activity coupled with processing demands elsewhere that combine to predict false memories.

A small number of studies have also utilized other neuroimaging methods to investigate the neural underpinnings of false memories. Using a misinformation paradigm and gray matter volume estimates, Zhu et al. (2016) found that hippocampal volume negatively predicted false memory rates, while right fusiform volume positively predicted false memory rates in younger adults. Such findings provide support for the multiple trace theory account of misinformation, as contextual information is posited to be stored in hippocampus, while post-misinformation traces are stored within cortical regions such as fusiform gyrus. A recent study from our group suggests that white matter microstructure also contributes to false memories. In a sample of healthy younger and older adults, we found that older, but not younger, adults with reduced white matter microstructure of the fornix exhibited higher rates of false recollection (Chamberlain et al., 2021a). Two studies have looked at the relationship between white matter microstructure and false memory errors (Chamberlain et al., 2021b, Fuentemilla et al., 2009). While Fuentemilla and colleagues (2009) found a significant relationship between the structure of the superior longitudinal fasciculus and semantic false memories in young adults, Chamberlain and colleagues (2021b) found that reduced microstructural white matter integrity in the fornix contributes to false recollection in older adults. Additional work using event-related potentials (ERP) suggests that parietal negativity distinguishes between true and false memories, which have been interpreted as faulty reconstructive processes (Gonsalves and Paller, 2000; Nessler and Mecklinger, 2003; Nessler et al., 2001). Finally, several studies using transcranial magnetic stimulation (TMS) have found that application of excitatory stimulation to frontal and anterior lobe reduces false, and not true, memories in younger adults (Boggio et al., 2009; Diez et al., 2017; Gallate et al., 2009), highlighting the role of these regions in false memory functioning. While more work is clearly needed to understand how structural, time course, and excitatory components relate to false memories, the foregoing studies offer novel insights to this question.

Consistent across univariate and multivariate analysis approaches, retrieval studies strongly suggest processing within primary sensory cortices plays a critical role in the detection of true memories, whereas processing within frontal-parietal cortices has consistently been shown to contribute to false memory errors. Specifically, research suggests that, irrespective of memory paradigm, processing related to item-specific sensory features of the original study episode are fundamental to the later identification of the information in a memory paradigm, as well as the later correct rejection of perceptually related, yet novel, information. When errors occur related to the presentation of related, yet novel information, research points to a role of higher order monitoring processes as an underlying mechanism leading to memory errors. Interestingly, despite a pivotal role in memory success, research suggests that functioning within the MTL does not directly contribute to false memories, but rather it is the interaction between MTL activity and processing within other components of the retrieval network that is critical to the occurrence of false memories.

ENCODING

While the majority of false memory studies have focused on retrieval processes, the role of encoding has also been regarded as a critical component in contributing to subsequent memory errors. However, in contrast to retrieval studies, it is generally difficult to isolate the neural processes that contribute to the formation of a specific false memory. For example, if gist builds over time, or if activity from several exemplars leads to the activation of the non-studied lure, then there is no single moment during encoding with which to examine a subsequent false memory error. Despite this limitation, a handful of studies have been able to explore the role of encoding in the formation of false memories (Baym and Gonsalves, 2010; Gonsalves and Paller, 2000; Gonsalves et al., 2004; Gordon et al., 2019; Kensinger and Schacter, 2005; Kim and Cabeza, 2007a; Kubota et al., 2006; Okado and Stark, 2005; Stephan-Otto et al., 2017; Wing et al., 2020) as well as the relationship between encoding to retrieval processes (Chamberlain et al., 2021; Lee et al., 2019; Wing et al., 2020; Ye et al., 2016; Zhu et al., 2019).

Similar to the conclusions reached in retrieval studies, encoding studies have stressed the importance of frontal, MTL, MTG, and sensory activation in accounting for differences in subsequent true and false memories. For example, using a modified DRM paradigm Kim and Cabeza (2007a) showed that, while regions involved in

semantic elaboration (left ventro- and dorsomedial PFC) and conscious item processing (bilateral occipitotemporal and occipitoparietal cortex) were involved in both true and false memory formation, true memories alone were associated with greater activity in PHG and early visual cortex (BA 18/17). The authors concluded that when richer, more fine-grained, encoding representations are formed, this will lead to a stronger retrieval trace able to endorse targets and reject lures. Supporting this idea, recent work from Naspi et al. (2021) using representational similarity analysis and a computational model of visual cortical processing (HMAX), found that reduced correspondence between neural patterns and computational patterns in early visual cortex and left inferior temporal gyrus was associated with subsequent false recognition. Such results suggest that poor encoding of perceptual information within sensory cortex contributes to memory errors during retrieval. This may be due in part to the lack of robust visual features stored in memory, leading participants to rely on gist when making their retrieval decision.

This importance of the encoding trace is also reflected in the results of misinformation studies. Specifically, misinformation studies suggest that if an individual is presented with two sources of information (original and secondary misinformation), the presentation that begets the greater amount of neural processing within ventral visual regions is that which is most likely to be remembered (Baym and Gonsalves, 2010; Gonsalves et al., 2004; Gordon et al., 2019; Okado and Stark, 2005; Stark et al., 2010). For example, Baym and Gonsalves (2010) found that greater activity throughout ventral visual regions during the original encoding event was associated with subsequent true memories as compared with false memories. The authors concluded that this increased activation during encoding may reflect the storage of more fine-grained details that supports accurate memory in the face of subsequent misinformation. Alternatively, Gordon et al. (2019) found evidence that both misinformation and subsequently corrected information resulted in equitable neural activity, suggesting that both accurate and misinformation were stored, thereby creating subsequent retrieval monitoring failures related to false memories.

While evidence is limited in understanding the role of the MTL and its subregions in this distinction, a handful of studies have shown that activation within the hippocampus and PHG to be associated with subsequent true as compared with false memories (Kim and Cabeza, 2007a; Wing et al., 2020; Zhu et al., 2019). Contrary to this finding, increased activity in nearby perirhinal cortex has been shown to predict subsequent false memories (Chen et al., 2019; cf. Okado and Stark, 2005). This difference may highlight the importance of item-specific processing within the hippocampus proper in guarding against false memory formation. The role of the hippocampus was further quantified with respect to false memories by Wing et al. (2020) using pattern similarity analysis during encoding. Specifically, they found that false memories for lures were predicted by the interaction of increased concept-specific encoding similarity in dorsal parietal and early visual processing regions and activation patterns within the hippocampus related to lure processing at retrieval. This study is one of the first studies to identify a role of hippocampal pattern differentiation in promoting accurate lure discrimination under conditions when cortical similarity is high among encoded objects. Certainly, more work, and perhaps high-resolution neuroimaging techniques, are needed in order to fully elucidate the role MTL subregions play in distinguishing subsequent memory veracity.

While processing in primary sensory cortices and possible MTL activity is critical to predicting true, as opposed to false memories, subsequent false memories have been associated with neural activity in the anterior cingulate cortex (ACC), parietal, and MTG at the time of encoding (Dennis et al., 2007; Garoff et al., 2005; Gonsalves et al., 2004; Kim and Cabeza, 2007a; Kurkela and Dennis, 2016; Okado and Stark, 2005). MTG activity is interpreted as reflecting encoding of semantic and perceptual gist that is later utilized when endorsing a lure that shares that same gist. With regard to frontal-parietal activation, while one study (Gonsalves et al., 2004) attributed ACC and parietal activity to heightened visual imagery at encoding that led participants to mistakenly think they perceived the lure, other studies have not offered an explanation of this activity. We believe it is worth noting that increased activity within this frontal region has been associated with subsequent forgetting in metanalyses (Kim, 2011). As part of the default mode network, activity in this region during memory encoding has been associated with mind wandering and lapses of attention that ultimately led to errors of omission in memory. Subsequent false memories may arise during this forgetting process, whereby in the absence of item-specific details, errors are made when evaluating a related lure at retrieval.

ENCODING RETRIEVAL SIMILARITY

Although encoding alone may not be the focus of recent neuroimaging work related to false

memories, several studies have examined the correspondence of neural patterns between encoding and retrieval using multivariate analyses. Specifically, the application of encoding retrieval similarity (ERS) analyses has sought to elucidate the overlap (or correlation) of neural information across memory phases, with an emphasis on that which supports veridical and erroneous memory decisions (Chamberlain et al., 2021a; Lee et al., 2019; Wing et al., 2020; Ye et al., 2016; Zhu et al., 2019). Not surprisingly, this work again highlights the critical role the visual cortex plays in differentiating true and false memories, with ERS studies linking stronger neural similarity in occipital regions to veridical, opposed to erroneous, memory retrieval (Chamberlain et al., 2021a; Ye et al., 2016; Zhu et al., 2019). For example, Ye et al. (2016) found that ERS within the lingual cortex was both greater for true as compared with false memories, as well as accounted for veridical memory strength. Similarly, Zhu et al. (2019) observed greater ERS associated with true memories as compared with false memories in lateral occipital regions. Such findings support and extend the observed univariate findings of greater sensory activation for true as compared with false memories during retrieval. Additionally, greater ERS for true as compared with false memories further support the sensory reactivation hypothesis, suggesting that false memories lack the richness of perceptual information transferred from encoding to retrieval, which is ultimately necessary for the endorsement of a true memory. Interestingly, when examining ERS at the item level, results from our lab (Chamberlain et al., 2021a) found that that ERS related to lures positively predicted false memory rates in both early and lateral visual cortices. Taken together, results suggest that retrieval-related reinstatement of encoding activity in the earliest of sensory cortices corresponds to veridical memories, whereby failures of this recapitulation are more likely to result in less confident memories and more memory errors.

ERS analyses also continue to highlight the role that frontoparietal regions play in false memories (Lee et al., 2019; Ye et al., 2016; Zhu et al., 2019). For example, Lee et al. (2019) found that higher category-level reinstatement in angular gyrus corresponded with false alarms to lures, whereas item-level reinstatement in the same region predicted correct rejections. This finding was interpreted with respect to the notion that category-level reinstatement reflects gist processing that leads to a general, but non-specific, feeling of oldness. Similarly, Ye et al. (2016) found that global encoding-retrieval similarity within the lateral parietal cortex was shown to support more general memory retrieval (i.e., both true and false memories), with the strength of ERS in this region correlated with the lure relatedness (e.g., semantic similarity). Given that two theories of false memory (spreading activation and fuzzy trace) attribute false memories to more generalized semantic processing, the idea that this processing is formulated during encoding and carried over to retrieval in consistent with this idea.

Ye et al. (2016) also found that the relationship between increased ERS in parietal cortex and decreased ERS in occipital cortex for lure trials was correlated with frontal processes, suggesting that reinstatement of gist-level processing, in the absence of item-specific details of past events, leads to a heightened recruitment of frontal monitoring mechanisms to resolve the discordant processing of the new stimuli. Looking back at the relationship between frontal activity and false memories exemplified during retrieval studies, it may be concluded that such upregulation of monitoring is related to false memory errors. This idea is highlighted in recent work from Zhu et al. (2019) who observed encoding-retrieval similarity associated with false memories as compared with correct rejections in occipital and frontal cortices. The authors suggest that this reflects the erroneous reinstatement of encoding features during lure processing at retrieval, thereby placing an increased demand on frontal monitoring processes. Taken together, the foregoing findings support the notion that sensory cortices recapitulate less information when a lure is being evaluated at retrieval than a target, thereby leaving degraded or incomplete memory traces that contribute to committing a memory error. At the same time, frontal and parietal cortex appear engaged in top-down processing in the presence of novel lure stimuli, both attending to the new features and engaging in monitoring conflict processes (see Figure 7.4).

This interplay between lower-level sensory activation and higher-order monitoring processing has also been observed in ERS studies that integrate both univariate and multivariate analyses. For example, Zhu et al. (2019) found that BOLD activity associated with lures positively predicted the discrepancy between ERS in frontal and occipital cortex, suggesting that higher order processes were necessary to resolve the discordant processing of the new stimuli. Additionally, Ye et al. (2016) found frontal activity accounted for the discrepancy between parietal activation and lateral occipital ERS associated with lure items. Such findings add support to the notion that cortical processes operate in tandem with one another when presented with novel information requiring mnemonic discrimination. Specifically, it appears that frontal monitoring mechanisms may be engaged in conjunction with parietal

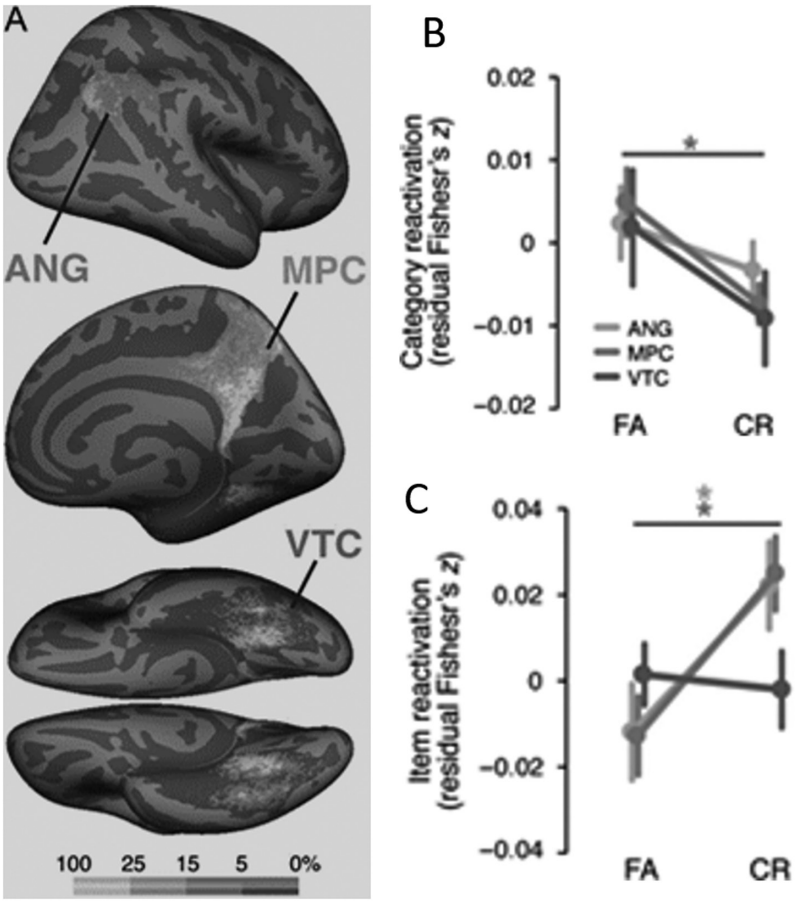

Figure 7.4 (A) Cortical reactivation underlying false alarms and correct rejections found in angular gyrus (ANG), medial parietal cortex (MPC), and ventral temporal cortex (VTC). Adapted from Figure 3 of Lee et al., 2019. (B) Greater category-level reactivation was associated with false alarms in medial parietal cortex. (C) Reduced item-level reactivation associated with false alarms in angular gyrus and medial parietal cortex. (Adapted from Figure 4 of Lee et al., 2019.)

control processes when presented with discordant sensory neural patterns. It is likely that frontal cortex is engaged during more generalized processing associated with monitoring and executive functioning, and that the type of information being recapitulated (i.e., neural patterns) is the same for both true and false memories within such regions. Further, as discussed previously, neural patterns may be relevant to the tested modality within other portions of cortex (such as visual features within the visual stream, and auditory signatures within auditory and semantic processing regions).

Consistent with the findings highlighted in the retrieval section, both the encoding and ERS evidence points to the need for a strongly encoded sensory representation of the studied information, followed by the ability to retrieve or reactivate this presentation when making memory decisions. Research across a number of analysis methods points to the need for a strong correspondence in the memory representation between encoding and retrieval supporting both higher hit and lower false alarm rates. This evidence is consistent with the sensory reactivation theory of memory that has been investigated for decades in memory research.

AGING

One domain where false memories are especially problematic is aging. Age-related memory impairment is well documented (Dennis and Cabeza, 2008; Park and Gutchess, 2005). While it is often assumed that age-related forgetting lies at the heart of this deficit, research shows that age-related increases in false memories are an equal contributor to age-related memory deficits (McCabe et al., 2009). Behavioral theories described above are often used to explain age-related increases in false memories, with emphasis placed on gist-based accounts of false memories (Brainerd and Reyna, 2002; Schacter et al., 1997b; Tun et al., 1998). There is a relatively small, but growing literature examining the neural basis of false memories in aging (Chamberlain et al., 2021a; Dennis et al., 2007, 2008, 2014, 2021; Dennis and Turney, 2018; Devitt and Schacter, 2016; Duarte et al., 2010; Fandakova et al., 2015, 2018; Giovanello et al., 2009; Gutchess et al., 2007; Paige et al., 2016; Webb and Dennis, 2019). Overall, the results from these studies build upon and emphasize many of the same findings identified in younger adult studies, as well as findings from more general investigations into age-deficits in veridical memories (Dennis and Cabeza, 2008; Maillet and Rajah, 2014).

Specifically, neuroimaging studies examining false memories have identified age deficits in univariate activity mediating true recollection in both the MTL and the visual cortex (Bowman and Dennis, 2015; Dennis et al., 2014a; Dennis et al., 2007, 2008; Duarte et al., 2010; Gutchess et al., 2007; Paige et al., 2016). Despite these overall activation deficits, older adults exhibit differentially greater activity within these regions for veridical as compared with false retrieval (Dennis et al., 2014a; Dennis and Turney, 2018; Webb and Dennis, 2019). Taken together, these results suggest that age-related deficits in processing veridical information, including fine-grain details that differentiate between studied and unstudied information within sensory cortices, likely contribute to age-related increases in false memories.

Taking a multivariate approach to the examination of false memories in aging, recent work from our lab has supported and extended much of these earlier findings regarding the critical role of sensory cortices in accounting for age differences in false memories. For example, a recent multivariate analysis from our lab (Bowman et al., 2019) identified age deficits in pattern classification analysis (MVPA) distinguishing targets and lures within early visual cortex (see also Dennis et al., 2021 for a related finding using RSA). Despite this deficit, the positive relationship between neural and behavioral discriminability did not differ across age groups. In contrast, age moderated this relationship in lateral occipital and fusiform cortices, such that increased classification accuracy predicted worse memory performance in older adults. An examination of single-item ERS on the same data (Chamberlain et al., 2021a) found that ERS for targets and lures was reduced with age throughout much of the ventral visual stream and the posterior hippocampus. The relationship between ERS of perceptual lures and false memories was again moderated by age such that item lure ERS positively predicted false memory rates in older, but not younger adults. Interestingly, we also found that a global ERS metric accounted for age deficits in single-item ERS, but did not account for false memory rates. These findings highlight the contribution of age-related reductions in ERS across multiple representational levels to false memories in healthy aging. Together, results suggest that aging reduces the fidelity of neural information associated with old items, with such information likely becoming more gist-like in later adulthood. Furthermore, as some visual cortex regions exhibit age-related moderations with behavior while others do not, the content of information maintained within such regions may vary across sensory regions and be altered by aging, becoming relevant to false memory processes with advancing years.

Related to age deficits in item-specific processing is that of increases in gist-based processing (Tun et al., 1998). To that end, research using memory tasks that place a high demand on both semantic and perceptual relatedness has found that, in aging, both true and false memories are mediated by activity within the middle and superior temporal gyri (Dennis et al., 2014a; Dennis and Turney, 2018; Dennis et al., 2007, 2008; Webb and Dennis, 2019), regions involved in semantic and gist processing (Saumier and Chertkow, 2002; Simons et al., 2005). Furthermore, work from our lab has shown that activity within these lateral temporal regions is predictive of individual differences in false memory rates in older adults (Dennis et al., 2014; Dennis and Turney, 2018; Webb and Dennis, 2019) (Figure 7.5).

Retrieval of schematic information in aging has also been linked to activity in medial PFC (Dennis et al., 2014a; Dennis and Turney, 2018; Duarte et al., 2010; Fandakova et al., 2018; Webb and Dennis, 2018), the same region that has shone to mediate false memories across a number of studies in young adults (see above). Similarly, age-related deficits within the frontal-parietal network have frequently been observed in false memory studies

(Bowman and Dennis, 2015; Dennis et al., 2014a; Fandakova et al., 2015, 2018), with most studies attributing this finding to age-deficits in monitoring-related memory processes (Mitchell and Johnson, 2009). For example, examining associative false memories, Fandakova et al. (2018) found that young, but not older adults modulated activity across cingulo-opercular regions for false alarms and low-quality correct rejections, consistent with the area's role in postretrieval monitoring. Many of the foregoing studies have also identified individual differences with respect to frontal-parietal recruitment linked to false memory errors (Dennis et al., 2014a; Dennis and Turney, 2018; Fandakova et al., 2015; Webb and Dennis, 2018). Combined with deficits in sensory regions processing item-specific details, results strongly support a role of both gist processing and deficits in monitoring in accounting for false memories in aging. The breadth of the results also speaks to the need to account for individual differences in task performance when examining brain activity supporting false memories in aging.

SUMMARY AND CONCLUSIONS

Overall, there is considerable consistency across studies regarding the neural basis of false memories. Specifically, during memory retrieval, the decision-making process underlying target endorsement and erroneous lure endorsement engage largely similar neural substrates. Yet, while lure "retrieval" mirrors target retrieval in many aspects, there is also much evidence suggesting that neural processing across the entire memory retrieval network does, in some manner, distinguish between true and false memories. One of the most consistent findings is found with processing differences within the occipital (i.e., sensory) cortex. Specifically, while univariate analyses often identify greater overall activation for true as compared with false memories, multivariate analyses highlight distinguishable patterns of neural activity within this region across the two trial types. These results are interpreted with respect to the amount and quality of prior item details that are (or can be) recapitulated at retrieval. This conclusion is further supported by ERS evidence showing that true memories elicit higher overlap in neural patterns across memory phases than do lure items, with results again speaking to the idea of recapitulation differences across trial types.

Given the richness of the original event, it is not surprising that, without this information, (i.e., in the presence of a related, but novel lure), additional monitoring and evaluation is necessary to make a (false) memory decision regarding the lure. While this is the interpretation regarding increased activation in superior frontal and parietal cortices for false as compared with true memories, this difference is not always reflected in multivariate analyses –that is, while multivariate classification analyses have reliably identified discrete patterns of neural activity for true as compared with false memories in sensory cortices, this has not been observed when assessing frontal activation patterns. Similar findings have been found with respect to MTL activity, with univariate studies often showing greater overall activation levels for true as compared with false memories, yet multivariate studies failing to identify discrete patterns of activation across the two mnemonic trial types. However, there is some evidence from structural and connectivity analyses suggesting when the MTL–PFC connection is disrupted, as with reduced microstructural integrity or reduced functional connectivity, the influence of frontal and MTL functioning to false memories becomes more crucial.

Encoding and ERS studies support the main conclusions from the retrieval literature. Whether it be through perceptual and semantic relatedness studies or misinformation paradigms, encoding results highlight the contribution of strong sensory signals of the event corresponding with veridical memories. Moreover, when gist level information or misinformation receives stronger encoding activation, false memories are more likely to occur. Like retrieval, limited evidence from encoding also suggests that greater activity in the hippocampus and PHG leads to truer, as compared with false, memories, with one study suggesting the opposite when assessing activation levels of perirhinal cortex. More work is certainly needed to understand what, if any, differentiating traits the MTL contributes to subsequent veracity differences. Similarly, ERS studies support the notion that sensory cortices recapitulate less information when a lure is being evaluated at retrieval than when a target is present, thereby leaving degraded or incomplete memory traces that contribute to the commission of a memory error. At the same time results again highlight the role frontal and parietal cortices play in top-down processing in the presence of novel lure stimuli, both attending to the new features and engaging in monitoring conflict processes.

Recent research has continued to advance our understanding regarding false memory errors and their neural correlates. Overall, findings to date support multiple accounts of false memories, including fuzzy trace theory in which verbatim information is lacking, resulting in gist-like signals, spreading activation account in which higher order processes are engaged to reconcile new

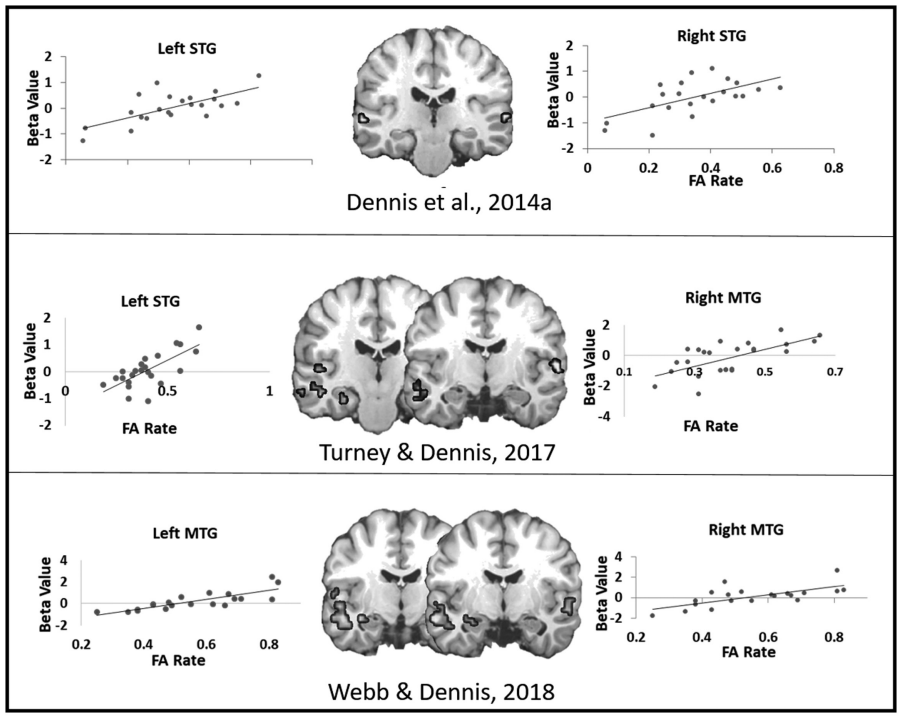

Figure 7.5 Modulation of superior and middle temporal gyrus (STG, MTG) activity as a function of false memory rates in aging. (Adapted from Dennis et al., 2014a; Turney and Dennis, 2017; Webb and Dennis, 2018.)

information, and global matching models that posit false memories occur due to differential "strength" of signals between encoding and retrieval. Future work should continue building on these theories by examining the multivariate underpinnings of the phenomenological processes of false memories. Future work should also continue to examine the interplay between brain regions identified in current work in order to understand subtle yet critical differences that underlie veracity differences in memory. Finally, as we continue to examine how the neural underpinnings of false memories are altered by age, it would be of great interest to identify how we might mitigate age-related increases in false memories via targeted interventions that reduce reliance on gist and enhance reliance on encoding-related details.

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